PLACENTATION AND OTHER PHENOMENA IN THE SCINCID LIZARD LYGOSOMA (HINULIA) QUOYI.

By H. Claire Weekes, B.Sc., Linnean Macleay Fellow of the Society in Zoology.

(*From the Department of Zoology, University of Sydney.*)

(Plates xxxviii-xl and twenty-three Text-figures.)

[Read 26th October, 1927.]

Contents.

I. Introduction.
II. Material and Methods.
III. Description of Material.
1. Period of "pro-oestrus".
2. Period of ovulation and fertilization.
3. Period of placental activity.
Stage A. Early development of the placentae.
Stage B. The stage of placental maturity.
Stage C. The placentae immediately prior to the birth of the foetus.
4. Period after birth.
IV. Comparison with the lizards, *Chalcides tridactylus*, *Lygosoma* (*Liolepisma*), *entrecasteauxi* and *Tiliqua scincoides* and with the marsupial, *Perameles*.
V. Theoretical Considerations.
VI. Summary and Conclusions.

I. Introduction.

In a "Note on Reproductive Phenomena in some Lizards" communicated to this Society in May, 1927, the placentation of the Scincid lizard *Lygosoma* (*Hinulia*) *quoyi* was described briefly and compared and contrasted with that of the Scincid lizards *Chalcides tridactylus*, *Lygosoma* (*Liolepisma*) *entrecasteauxi* and *Tiliqua scincoides* and with that of the marsupial *Perameles*. It is proposed to describe the placentation of *L. quoyi* and to discuss its relationship with that of the three above-mentioned Scincid lizards and of the marsupial *Perameles* in more detail in this communication.

In a previous paper (Harrison and Weekes, 1925) in which the occurrence of the placentation of the Scincid lizard *L. entrecasteauxi* was described, *L. quoyi* was mentioned, specimens of both having been collected at Barrington Tops during January and February, 1925, by the members of a party from the University of Sydney, under the leadership of Professor Harrison. In this paper (p. 471) it was stated that examination of pregnant females of *Trachysaurus rugosus*, *T. scincoides*, *L. quoyi*, *Egernia striolata* and *E. whitei* revealed "highly vascularized external allantoic and uterine walls with their respective circulations in close apposition but no marked placental area such as is described below" (for *L. entrecasteauxi*). A study of the condition in *L. quoyi* has shown that there is a very definite type of allantoplacenta present, although there is not the same degree of external differentiation of the uterine placental area. A further study has shown that a

somewhat similar placental condition occurs in *E. striolata* and *E. whitei* and probably also in *T. rugosus*.

Definite placentation among lizards has now been recorded in *Chalcides tridactylus* and *C. ocellatus* by Giacomini (1898) and (1906) respectively; in *Tiliqua scincoides* by Flynn (1923); in *Lygosoma* (*Liolepisma*) *entrecasteauxi* by Harrison and Weekes (1925); in *Lygosoma* (*Hinulia*) *quoyi*, *Egernia striolata* and *E. whitei* by Weekes (1927); and omphaloplacentation in *T. scincoides* by Weekes (1927). In addition Haacke (1885) mentions certain relations between the wall of the uterus and that of the yolk-sac in *Trachysaurus rugosus*. It is probable that a further investigation of the viviparous reptiles will reveal many interesting phenomena with regard to placentation.

I wish to thank Professor L. Harrison, in whose department this investigation was carried out, for the personal interest he has taken in the work and for the help he has given; Dr. I. M. Mackerras for specimens of *L. quoyi* collected at Barrington Tops; Mr. J. Hopson for collecting and forwarding material; Miss L. Wood, Mr. W. Graham, Mr. G. Vance and Miss B. White for help in collecting material; the Department of Zoology, University of Sydney, for grants covering the cost of collecting.

This investigation was begun under a Science Research Scholarship of the University of Sydney, and continued after my appointment as a Linnean Macleay Fellow of this Society.

II. Material and Methods.

Specimens of *L. quoyi* containing young were collected from Barrington Tops, 150 miles north of Sydney, at a height of 4,500-5,000 feet, during January, February and December, 1925; from Mount Kosciusko, 300 miles south of Sydney, at a height of approximately 5,000 feet, during November and December, 1925; from the Blue Mountains, 70 miles west of Sydney, at a height of approximately 3,000 feet, during January and February, 1927; from Sydney, at sea level, during November and December, 1925, and September, October, November, December, 1926, and January, 1927; from Kiama, on the Coast, 70 miles south of Sydney, during January, October and November, 1926.

The study of *L. quoyi* is interesting apart from the factor of placentation. The specimens collected from Barrington Tops and Mount Kosciusko, at a height of approximately 5,000 feet, differ from those collected at sea level, although each type has been identified as *Lygosoma* (*Hinulia*) *quoyi*. Those collected at Barrington Tops and Mount Kosciusko have an average length of five inches and the pregnant females contain from three to five young; those from the coast are much larger measuring from ten to thirteen inches and the pregnant females contain from five to nine young. The difference in scale marking between the two types of lizard is slight, since members of the same type vary among themselves, and the placentae in both are identical. The difference in the number of young carried during the gestation period seems to depend on the size of the parent lizard, although this conclusion may not be correct, since the increase in the size of the adult is naturally followed by a corresponding increase in the size of the embryo, those of the mountain type measuring approximately 3 cm. at the time of birth, and those of the coastal type measuring approximately 5 cm. Those females collected at the Blue Mountains, at 3,000 feet, were intermediate in size between the two above described types measuring on an average eight inches in length and containing from three to five young.

The reason for the difference in the size of the mountain and coastal types of lizard is not apparent, but in January, 1927, an intermediate type was collected at a height of 3,000 feet indicating that altitude may be the determining factor, and that the change from the small to the large type of lizard may be gradual as the altitude decreases.

L. quoyi is essentially a water loving animal and always lives near a creek or water hole. The flat marshy land at Barrington Tops and Mount Kosciusko with its network of small watercourses is infested with them. They live in holes in the banks of the watercourses, and at the coast they live in similar holes in the banks of coastal streams.

As mentioned, pregnant females were collected from Mount Kosciusko during November and December, 1925, and from Barrington Tops during January and February, 1925. They were first collected from Mount Kosciusko on the 14th November and the contained embryos are estimated to be one week old, hence fertilization occurred during the first week in November. The females collected from Barrington Tops during the first week in February contained embryos which were within a few days of hatching, but since it is at present unknown to the writer whether the times of the fertilization of the ova of the lizards at Mount Kosciusko and Barrington Tops correspond, the exact length of the gestation period of the mountain type is unknown.

Females of the coastal type collected at Sydney on 10th September and 7th October, 1926, had the ova still within the ovaries. On the 18th October females were collected which had the ova in early stages of segmentation within the oviducts, so that fertilization in these lizards occurred in the middle of October, which is two weeks earlier than at Mount Kosciusko. Lizards were collected from the same locality at Sydney, from the time of the fertilization of their ova until the time of the birth of the young, which was the second week in January. Hence the development of *L. quoyi* at sea level covers a period of approximately three months. Females were kept alive until the young were born and thus *post partum* stages were obtained.

Summarizing the above, specimens of *L. quoyi* were collected at a height of 4,500-5,000 feet which contained embryos in stages of development ranging from the first week after fertilization until the time of hatching; specimens were collected at sea level at all stages ranging from the condition of non-pregnancy to the condition after birth.

All material was fixed in Bles' Solution (90 parts of 70% alcohol, 7 parts of 5% formol, and 3 parts glacial acetic acid). The ventral body wall of each female was cut longitudinally to expose the oviducts, the female with young *in situ* then being immersed in the fixative. It is not advisable to leave the material in the fixative indefinitely as Bles' Solution hardens yolk.

As most of the material contained much yolk it was found difficult at first to get satisfactory results when infiltrating without using the method of double embedding in celloidin and paraffin, a method which has many disadvantages when dealing with yolky material. Embedding in paraffin alone was successful when the following precautions were taken: (*a*) to secure a thorough dehydration of the material, the latter, if bulky, being passed through many changes of absolute alcohol over a period of at least two days; (*b*) to use pure clearing agents, preferably xylol or cedar wood oil. As an inferior quality of xylol is usually sold which gives a white precipitate when mixed with alcohol, it is advisable to use cedar wood oil. However, if the xylol will mix with 70% alcohol without

giving a permanent precipitate, it will give better results than the cedar wood oil. Cedar wood oil which is sold as pure often contains water, but it was found that by mixing the oil with a fair quantity of anhydrous copper sulphate, shaking well and allowing to stand for twenty-four hours and then filtering, the water and other impurities were removed and the oil made perfect for use; (*c*) to infiltrate gradually, leaving the cleared material at room temperature in a solution of the clearing agent saturated with paraffin for about twenty-four hours, then leaving it another twenty-four hours at about 30° C., more paraffin having been added, and finally passing it through several changes of pure wax inside the paraffin bath for a few hours before embedding. If the material became brittle a shorter time in the solution of clearing agent and wax was allowed. I have successfully cut lizards' ova 8 mm. in diameter when these precautions were taken.

When staining, if the yolky sections washed off the slides this was usually due to imperfect floating out of the wax ribbons on the slides, and imperfect drying of the ribbons after floating out. The floating out was most successful when done gradually and at a moderate temperature. Floating out on the top of a paraffin bath is not a perfect method as the copper bath is usually much too hot and the floating out dangerously rapid. I use a large piece of thick plate glass arranged at a suitable distance above an electric light bulb, so that the glass is just warm and the slides may be left on it for hours without damage, until they are thoroughly dry. This method of dry heating eliminates the danger of imperfect fixation due to a moist atmosphere.

It was found more important to take these precautions than to use a greater quantity of egg albumen, since ribbons that are well floated out and thoroughly dried should not leave the slides even when passed into 0·5% acid alcohol.

For an examination of anatomy the material was stained in bulk in carmalum. For histological work, sections were stained in Delafield's haematoxylin and counterstained in eosin.

III. Description of Material.

The material is described in four parts. The first part covers the period of "pro-oestrus", the second the period of ovulation and fertilization, the third the period of placental activity and the fourth the period after birth. The period of placental activity is divided into three stages, Stage A presenting the early development of the placentae and covering the first two weeks of the gestation period; Stage B presenting the mature placentae, and covering the following eight weeks of the gestation period; and Stage C presenting the placentae immediately prior to the birth of the foetus and covering the last two weeks of the gestation period.

The description of the periods of "pro-oestrus" and of ovulation and fertilization are based on examinations of lizards collected at sea level. However it is more than probable that during these periods the condition of the reproductive organs of females inhabiting the mountain regions is the same.

The descriptions of the period of placental activity and of the period after birth are based upon an examination of both types of lizard, and as the placentae of both are identical no distinction is made between them.

1. *Period of "pro-oestrus".*

As mentioned above, females, which presumably had not copulated, were collected at Sydney on 10th September, 1926. The reasons for assuming that copulation had not taken place are: when collected the ova were still within

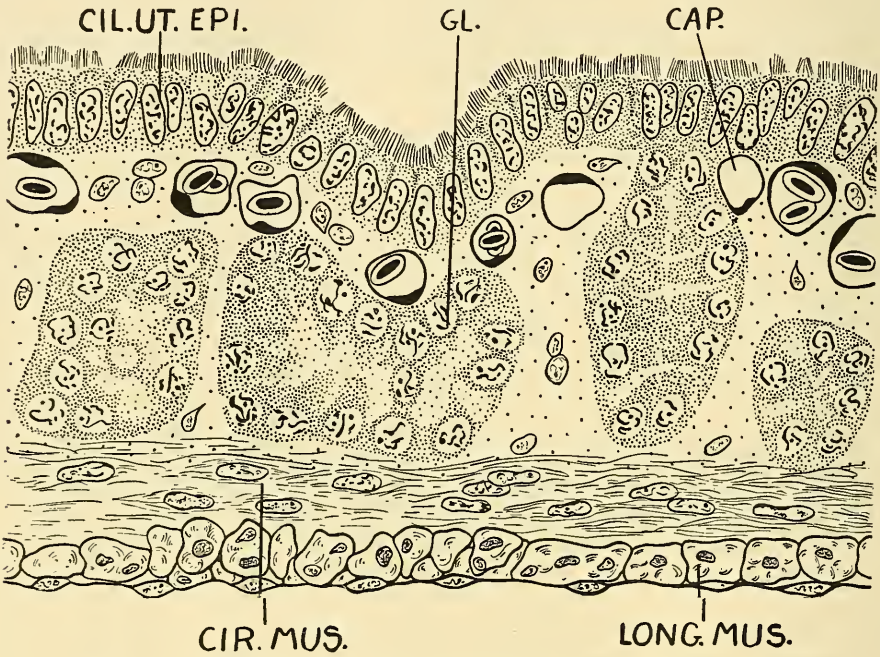
the ovaries and had not reached maturity, the largest ovum measuring 6 mm. in diameter, the measurement at maturity being approximately 13 mm.; also, during the beginning of September the weather is not warm enough to bring the lizards out in any number, only three being caught on 10th September after searching for two days; again, fertilization does not take place until the middle of October and one would expect copulation to occur nearer the time of fertilization than 10th September, which is five weeks earlier, and although actual copulation was not observed during the middle of October, it is extremely probable that it occurred then, since the lizards were observed living in pairs, a male with a female, the females being easily distinguished by their greater girth due to the presence of the enlarged ovaries.

The female reproductive organs consist of a right and a left ovary each equally well developed, and two oviducts which open separately into the cloaca. Each ovary is situated at the middle of the length of the corresponding oviduct. In each of the two females collected on 10th September, the right ovary was more anteriorly situated than the left, and the stomach was on the left side above the left ovary and closely pressed against it. In one female there were four large ova in each ovary, in the other there were four large ova in the right ovary and three in the left. This species of lizard has only one breeding season each year and the development of the ova is regulated accordingly, so that there is little gradation in the size of the ova at this stage, but a marked contrast between a number of small ova, all at approximately the same stage of development, to a number of larger ova, also at approximately uniform stages in development. At this stage these large ova have the same structure as that described for the developing ova of *Lacerta agilis* (Hett, 1924), where the follicle cells are of two varieties, some being enormously enlarged and the others comparatively small.

The oviducts are pleated, twisted and flattened against the dorsal body wall of the lizard, the average length of an extended oviduct being 5 cm. The width varies considerably, from 5 mm. to 2·5 mm. owing to an indication of division into "incubatory chambers", which is due to the failure of the oviducts to regain completely their natural shape after the preceding year's gestation period. Giacomini (1891) wrote that these chambers are evident in the oviducts of *C. tridactylus* three months after birth. In *L. quoyi* it seems that they never completely disappear.

The structure of the oviducts in these females is regarded as normal and only variations from it, found in the oviducts during the period of placental activity, are considered placental modifications. In section the wall of the oviduct at this stage is more or less uniform in structure throughout its length with the exception of the extreme anterior end which is modified for the reception of the ova. The arrangement of the tissues of the oviductal wall seems uniform for lizards in general, as it occurs in every species examined by the writer as well as in *C. tridactylus*. The wall at the anterior end is thrown into folds, is comparatively thin and the epithelium lining the lumen of the oviduct in this region is glandular and ciliated, consisting of deep columnar cells which are much larger than those lining the rest of the lumen. The wall of the remaining part of the oviduct (Text-fig. 1) consists of the following layers: an external layer of peritoneum; a thick muscular coat consisting of an outer coat of longitudinal muscle and an inner coat of circular muscle; a thick mucous membrane in which glands are embedded and which is lined by ciliated epithelium. The glands embedded in the mucosa are simple or branched and open into the lumen by short narrow mouths.

They are saccular, the cells being composed of vacuolated cytoplasm with small oval nuclei arranged round the periphery, and the cell walls being usually indistinct. Many of the nuclei are undergoing mitosis, indicating the growth of the glands. The epithelium lining the lumen of the oviduct is composed of narrow ciliated cells, closely crowded together, with many of their nuclei also dividing.



Text-fig. 1. Section of the wall of the oviduct of a non-pregnant female. CAP., capillary; CIL. UT. EPI., ciliated uterine epithelium; CIR. MUS., circular muscle; GL., gland; LONG. MUS., longitudinal muscle. × 706.

The active cell division in the epithelium and glands indicates a "pro-oestrus" condition. The ordinary stimulus is certainly not copulation, since the ova in the females under discussion are at a stage about five weeks prior to ovulation, and it is extremely unlikely, as indicated above, that copulation has taken place. It is more likely that the stimulus is an external periodical one in which temperature is the main factor. That the breeding season of *L. quoyi* is influenced by climatic conditions is evident from the fact that the lizards inhabiting the warmer regions at sea level, Sydney, are at least two weeks earlier in their sexual season than those inhabiting the colder regions at Mount Kosciusko, 300 miles south of Sydney and with later seasonal changes.

2. *Period of ovulation and fertilization.*

On the 7th October, females containing ova at a stage prior to ovulation were collected from the same locality as on the 10th September. The ova had reached their maximum size and were packed with yolk. The membranes correspond with those described by Hett (1924) for *Lacerta agilis* at this stage, the cells of the

follicular epithelium being uniform in size and much smaller and flatter than those surrounding the younger ovum described above. There is a thicker band of thecal connective tissue in which numerous large blood vessels are present.

The oviducts have reached the final stage of preparation for the entrance of the ova. Each is roughly divided into three regions, namely, the anterior end described above, the more extensive middle region containing the majority of the glands, and the extreme basal region leading to the cloaca containing no glands and having its wall deeply convoluted. In section these regions differ somewhat from the corresponding regions of the oviducts of females collected four weeks earlier (10th September). At the anterior end the epithelial cells lining the lumen of the oviduct are markedly glandular and their free surfaces are covered by a thick secretion obviously derived from them and serving to facilitate the entrance of the ova. In the middle region the glands are most numerous and their cells are full of secretion and are distended until the central cavity is obliterated, thus indicating a period of glandular activity. The nature of the secretion from these glands is not apparent. At first, from the abundance of the glands and their position in the middle region of the oviduct, it was naturally supposed that they were for the secretion of albumen, but an examination showed that there is no sign of albumen surrounding the ovum after its passage into the oviduct or at any stage in its development. With the stretching of the "uterus" upon the entrance of the ova and the consequent squeezing of the glands, their secretion is forced out into the surrounding tissues of the uterus and some of it passes between the muscle layers and in stained material is identical in appearance with the substance of the shell membrane. The shell membrane is occasionally found adhering to the mouth of one of the glands when it has been torn away from the rest of the uterine wall, and a substance similar to it is present in the mouth of the gland. The cells of the epithelium lining the lumen of the oviduct in this region are also full of secretion, their cilia being matted together by the exuded secretion which is thought to be for the general purpose of lubrication.

It is not definitely known to the writer whether the process of ovulation in *L. quoyi* depends on some physiological stimulus such as the act of copulation, or whether it is independent of such stimulus; also, whether the liberated ova pass into the body cavity and thence into the oviduct with the aid of ciliary action, or whether they pass directly into the oviduct as a result of the latter actively clasping the ovum while still in the ovary.

As in other animals it is usual for the ova in each ovary to pass into the oviduct on the corresponding side, but a female was collected which had received an injury on the left side, damaging the left oviduct, so that, when ovulation took place, the mature ova, five in number, passed into the right oviduct. The liberation of ova from both ovaries was indicated by the presence of two burst follicles in the left ovary and three in the right. The five ova in the right oviduct were so tightly squeezed as to bend the oviduct completely out of position. The passage of ova across the body cavity is not uncommon among mammals, having been recorded for mammals "with a bicornuate uterus becoming pregnant in the uterine horn on the side opposite to that on which the ovary had discharged" (Marshall, 1910, p. 136).

When the ovum enters the oviduct and is fertilized, it becomes surrounded by a thin shell membrane which is divided into three layers composed of matted fibres. The uterus surrounds each egg as an expanded chamber called by Giacomini the "incubatory chamber". The wall of each incubatory chamber is uniform in

thickness measuring approximately 0·025 mm. and hence being much thinner than the wall of the uterus of a non-pregnant female. This decrease in thickness is due to the stretching of the uterus on the entrance of the eggs. Owing to this stretching, the coats of longitudinal and circular muscle are compressed into a thin band of tissue and the glands, which are swollen and saccular in the uterus of a non-pregnant female, are greatly compressed at this stage.

The epithelial cells lining the mucosa are much larger and not as crowded as in the non-pregnant condition, and are of uniform size over the entire area of the incubatory chamber.

There is a curious substance surrounding the ovaries after ovulation, which, in prepared sections, has the appearance of a deep blue coagulum mixed with blood clot containing corpuscles and numerous small round cells.

Immediately after ovulation the ruptured follicles are visible as large white flat oval sacs, each with the cicatrix present as a median longitudinal groove. However, a few days after ovulation they become smaller, spherical, yellow and richly vascular, the alteration in the appearance of the follicles being due to the presence of a corpus luteum in each, the growth of which is rapid, each follicle being completely filled with luteal cells a few days after ovulation. It is not probable that the corpora lutea have any influence on the retention of the ova of reptiles comparable with their supposed function in mammals, since they occur in ovaries of the oviparous lizard *Lacerta agilis*, which lays its eggs immediately after their passage down the oviducts (Hett, 1924).

3. *Period of placental activity.*

Stage A. *Early development of the placentae.*

Twenty females were collected containing young embryos with placentae at early stages in development, nine at Mount Kosciusko, eight at Sydney and three at Kiama. Of the nine from Mount Kosciusko, seven contained three young, one five and the remaining one six; of the eight from Sydney, four contained six, two seven and two eight; of the three from Kiama, one contained six, one seven and one eight. In every case where a female contained an even number of young, half were in each oviduct, and where a female contained an odd number of young the right oviduct held one more than the left. This arrangement of embryos was found to be the same in all lizards collected during the rest of the gestation period.

In the paper on the placentation in *L. entrecasteauxi* (Harrison and Weekes, 1925, p. 472) the authors wrote that "it seems remarkable that the number should be odd in every one of nine examples, and we cannot find any explanation for this condition", also, "of the six females examined, four had more embryos in the right oviduct than in the left". Taking into consideration the conditions in both *L. entrecasteauxi* and *L. quoyi*. it seems that there is a tendency for the female to contain an odd number of embryos, and for the right oviduct to contain more than the left. This may be due to the fact that the stomach of the non-pregnant female is almost invariably on the left side and closely pressed against the left ovary thus possibly interfering with the number of ova developing in this ovary.

The developing embryo is dorsal in position with regard to the parent and lies with its head directed mesially whether the embryo be in the right or left oviduct. The embryos in the one female are not all at identical stages of development, but the range of difference is negligible, *L. quoyi* resembling *L. entrecasteauxi* and not *C. tridactylus* in this respect. The uterus surrounds each egg as a thick

white envelope which persists as the expanded incubatory chamber on the extraction of the egg. These chambers are connected each to each by a short, narrow, strap-like portion of the uterus which is deeply folded. Occasionally the uterus is pigmented, the pigment being sometimes scattered over the surface of each incubatory chamber, but usually restricted to the dorsal body wall of the parent. The uterine wall shows as a smooth, semi-transparent membrane whose uniformity is broken only by its thick opaque blood vessels, since there are no villous foldings such as occur in *C. tridactylus* and *L. entrecasteauxi*. However, when viewed through the binocular microscope the uterine wall is seen to be covered by numerous branched glands (Text-fig. 2, A and B), which are homologous with the saccular glands in the uterine wall of the non-pregnant female (described above). They are present throughout the development of the embryo and are outstanding and characteristic.

The vascularization of the wall of the incubatory chamber of *L. quoyi* is on the same plan as that of *L. entrecasteauxi*. A single large artery and vein run longitudinally along the dorsal wall of each uterus, the artery giving off branches which pass transversely round the uterus to the base of the yolk-sac of the contained blastocyst, where they break up into a rich network of capillaries, and the vein receiving branches which also pass round the incubatory chamber from the base of the yolk-sac, parallel to and roughly alternating with the arteries (Text-fig. 2B). The villous folds in the wall of the uterus of *L. entrecasteauxi* are fed by short branches from the main artery and vein and by branches from the branch arteries and veins. In *L. quoyi* the allantoplacental region is similarly vascularized.

In the early stages of development the uterus fits closely round the contained embryos and keeps them in a fairly steady position, but with the preparation for allantoplacentation a more perfect state of fixation results when the cells of the chorion attach themselves to the epithelium of the uterus. However, before this occurs the intervening shell membrane must disappear and in early stages of development the chorionic cells appear to attack and absorb it. When the allantoplacenta is mature there are often areas where a thin remnant of membrane can be detected between the uterus and the modified chorion. The expansion of the growing embryo aids the chorionic cells in their destruction of the shell membrane by causing it to break and gradually fall away from the sides of the embryo taking up a position at the base of the yolk-sac in the form of a flat fibrous pad. This may be the "nodule" which occurs at the base of the yolk-sac of the embryos of *C. tridactylus*, and which Giacomini (1891) terms the vitelline membrane.

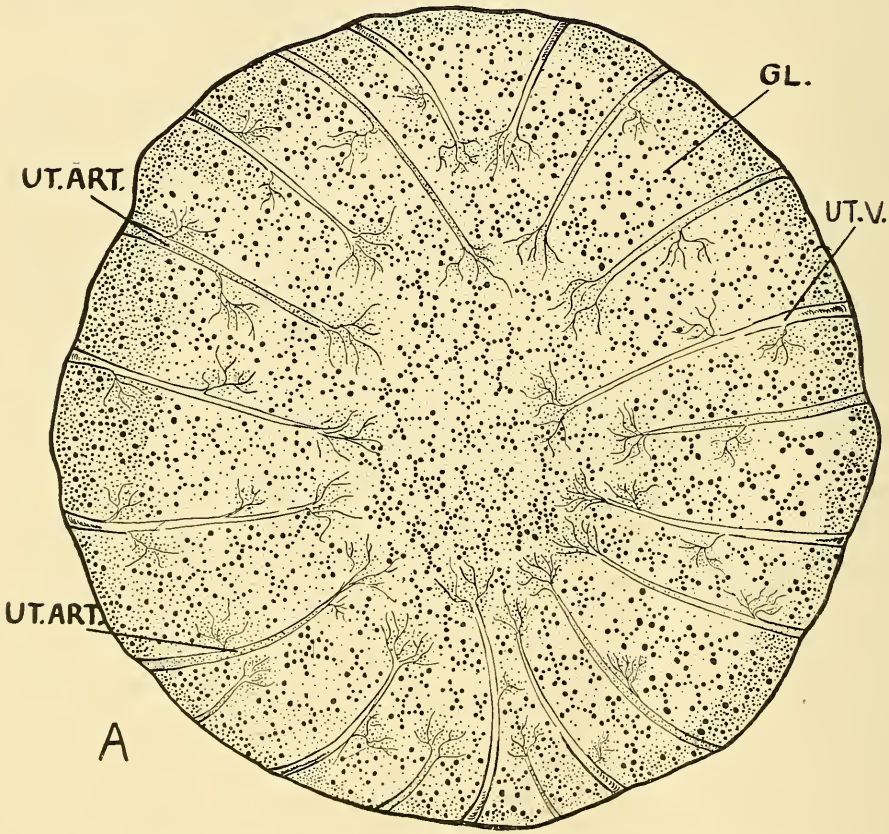
In *L. quoyi* the vitelline membrane is delicate and almost imperceptible and could not possibly be confused with the shell membrane.

Of the two placentae the omphaloplacenta is the first formed, since its requisites from the embryo, namely the chorionic ectoderm and a vascularized yolk-sac, are formed early in development, whereas the allantoplacenta, depending as it does on the presence of an allantois of sufficient extent to lie immediately under the chorion, is comparatively late in its development.

The Omphaloplacenta. The embryos which show the earliest signs of omphaloplacental modification are approximately one week old (Text-fig. 3, A), their average length being 5 mm. Each has turned on to its left side, its head being flexed and its body slightly curved. The amnion is completed and the allantois present as a small swelling at the posterior end of the embryo. There

are three gill slits and approximately thirty somites. The chorionic ectoderm completely surrounds the blastocyst and the extra-embryonic mesoderm extends over a small area at the surface of the yolk-sac, which is entirely lined by endoderm.

Although there are indications of foetal omphaloplacentation at this stage, the uterine wall is as yet unmodified. In all earlier stages the development of the extra-embryonic tissues is normal, the chorionic ectoderm cells being small and in all respects resembling those in the chorion of oviparous lizards, but at this stage the chorionic ectoderm at the base of the yolk-sac is slightly modified with the beginning of omphaloplacentation and the further growth of the extra-



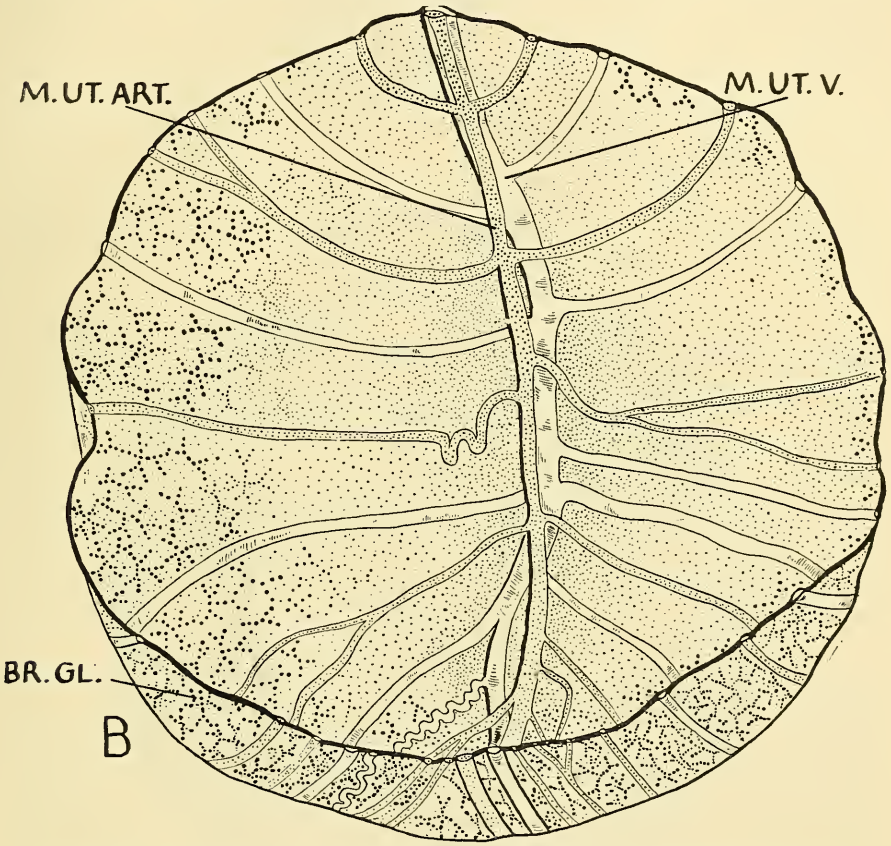
Text-fig. 2A. Incubatory chamber cut in half horizontally. Dorsal view of ventral half showing the termination of the uterine arteries and veins in the region of the base of the yolk-sac of the contained blastocyst, × 7·5; GL., gland; UT. ART., uterine artery; UT. V., uterine vein.

embryonic mesoderm is abnormal. In the former case, a few of the cells of the chorionic ectoderm at the lower pole multiply and become enlarged until a small area of enlarged cells is formed (Text-fig. 3B and 4).

Occasionally there is more than one centre of modification, but each is small and they gradually join together to form a single area. As the development of the embryo proceeds and the omphaloplacenta approaches maturity, the modification

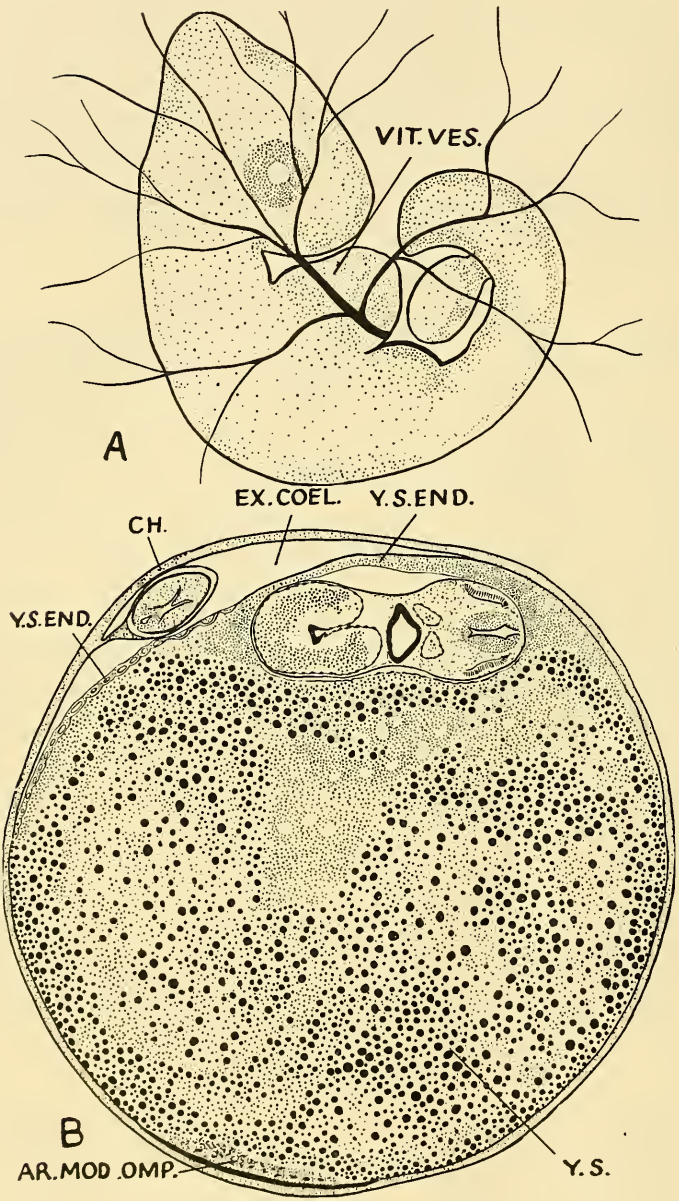
of the chorionic ectoderm spreads over the entire under surface of the yolk-sac, until a continuous sheet of moderately large columnar cells is formed.

In the embryos selected for description the area of modified ectoderm measures approximately 0·8 mm. in diameter by 0·1 mm. in height, being thickest at the centre (Text-fig. 4). It consists of a mass of deeply staining cytoplasm containing irregularly arranged nuclei, there being no definite cell boundaries present, even at the edge of the area where it merges into the unmodified chorionic ectoderm which covers the rest of the yolk-sac. The yolk-sac endoderm immediately overlies and mingles with the modified ectoderm and consists of a similarly staining cytoplasm with scattered nuclei. The cytoplasm of the ectoderm is denser than that of the



Text-fig. 2B. Ventral view of dorsal half showing the main uterine artery and vein, × 7·5. BR. GL., branched gland; M. UT. ART., main uterine artery; M. UT. V., main uterine vein.

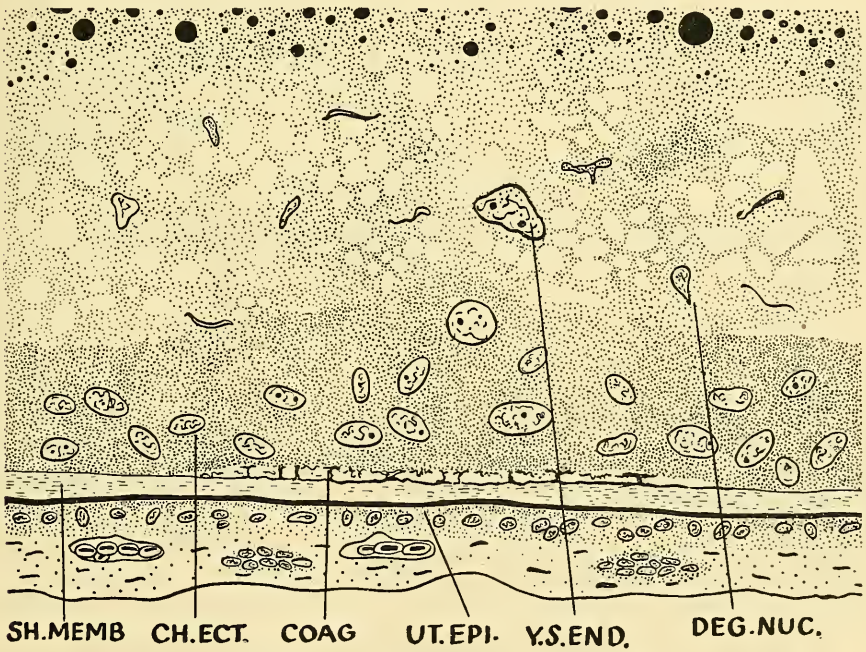
endoderm, which is vacuolated and has the appearance of having been mixed with a fluid which coagulated during the process of fixation (Text-fig. 4), and hence the line of junction between the two cytoplasmic regions is evident. The nuclei embedded in the ectodermal cytoplasm are large and irregular in shape, with no outstanding characteristics, and are easily distinguished from the endodermal nuclei, which are larger when healthy but which are mostly degenerating, many



Text-fig. 3. A, embryo approximately one week old, × 21·5; B, transverse section of blastocyst containing an embryo about one week old, showing the position of the area first modified for omphaloplacentation, × 11; AR. MOD. OMP., area modified for omphaloplacentation; CH., chorion; EX. COEL., extra-embryonic coelome; VIT. VES., vitelline vessel; Y.S., yolk-sac; Y. S. END., yolk-sac endoderm.

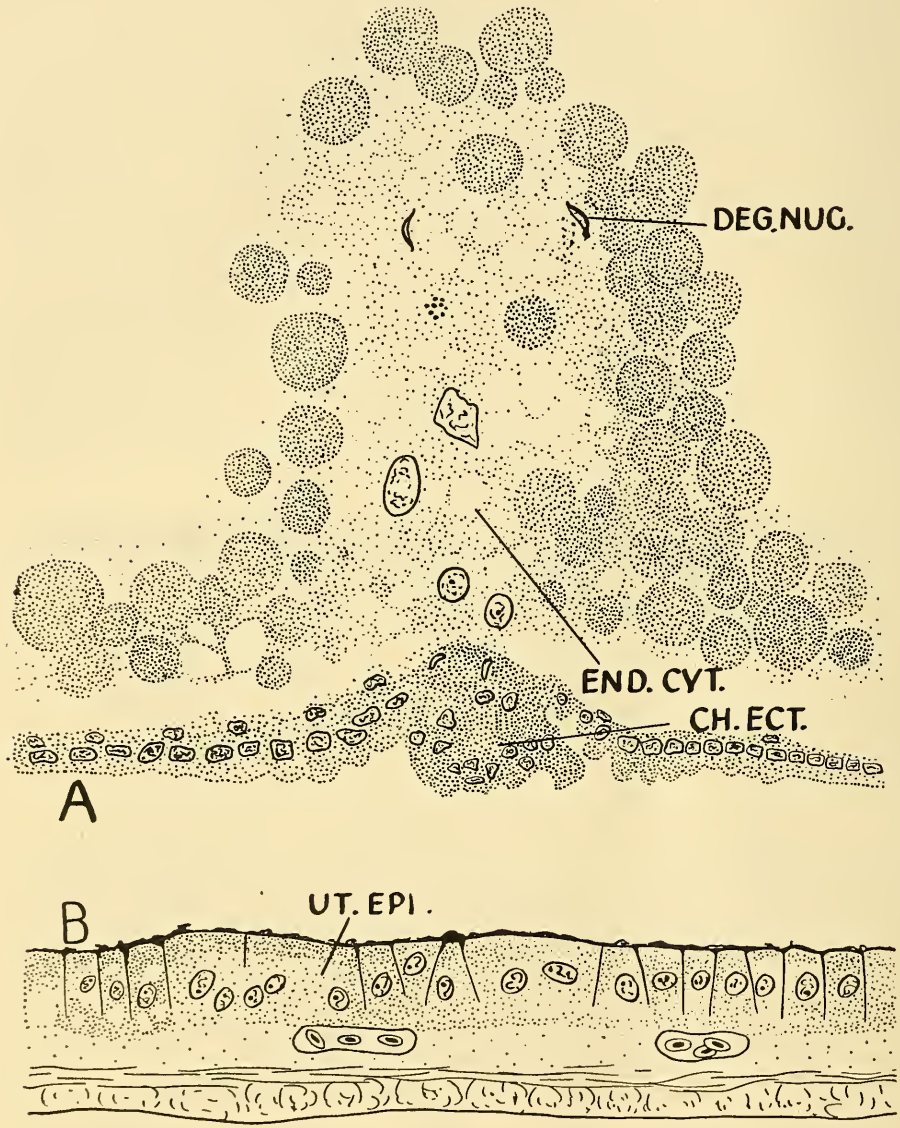
having been reduced to scattered groups of granules. The shell membrane underlies the chorionic ectoderm and between them is a gap which is partly filled with a coagulum stained deeply by haematoxylin, and thought to be maternal secretion passed through the shell membrane. It is possibly the presence of this secretion in the protoplasm of the yolk-sac endoderm which gives the latter its peculiar appearance. The uterine wall is pressed closely against the shell membrane and, as stated, shows no indication of placental modification.

In embryos taken from a female collected during the second week of pregnancy, the chorionic ectoderm cells are modified over a considerable area of the yolk-sac, but the original centre of modification is evident at the middle of the base of the yolk-sac where the cells are especially large and where the plug of endodermal cytoplasm is still present (Text-fig. 5, A; Pl. xxxviii, fig. 1). Some of the chorionic ectoderm cells are enlarged more than others, but are only about one-third the height they eventually attain. They are narrow but definite, with their free surfaces rounded and often bulging into peculiar shapes (Text-fig. 5, A, CH. ECT.; Pl. xxxviii, fig. 1). The nuclei vary in size sometimes almost filling the cell and they are arranged at the cell bases, staining deeply and standing out from the rest of the cell cytoplasm. The cells are closely attached to an underlying layer of yolk-sac endoderm, the cells of which are smaller than the ectoderm cells and lie at the bases of the latter with the appearance of dovetailing. They are so closely attached to the ectoderm cells that, when the layer of ectoderm is torn away



Text-fig. 4. Section of the omphaloplacental region, Stage A, showing the area of modified tissue, × 511. CH. ECT., chorionic ectoderm; COAG., coagulum; DEG. NUC., degenerating nucleus; SH. MEMB., shell membrane; UT. EPI., uterine epithelium; Y. S. END., yolk-sac endoderm.

from the overlying yolk-sac in the preparation of material for sectioning, the endoderm cells come away with it. The structure of the mass of endodermal cytoplasm at the approximate middle of the base of the yolk-sac is unchanged.



Text-fig. 5. A, section of the foetal portion of the omphaloplacenta of embryos collected during the second week of the gestation period, × 562; B, section of the maternal portion of the omphaloplacenta, × 562; DEG. NUC., degenerating nucleus; CH. ECT., chorionic ectoderm; END. CYT., endodermal cytoplasm; UT. EPI., uterine epithelium.

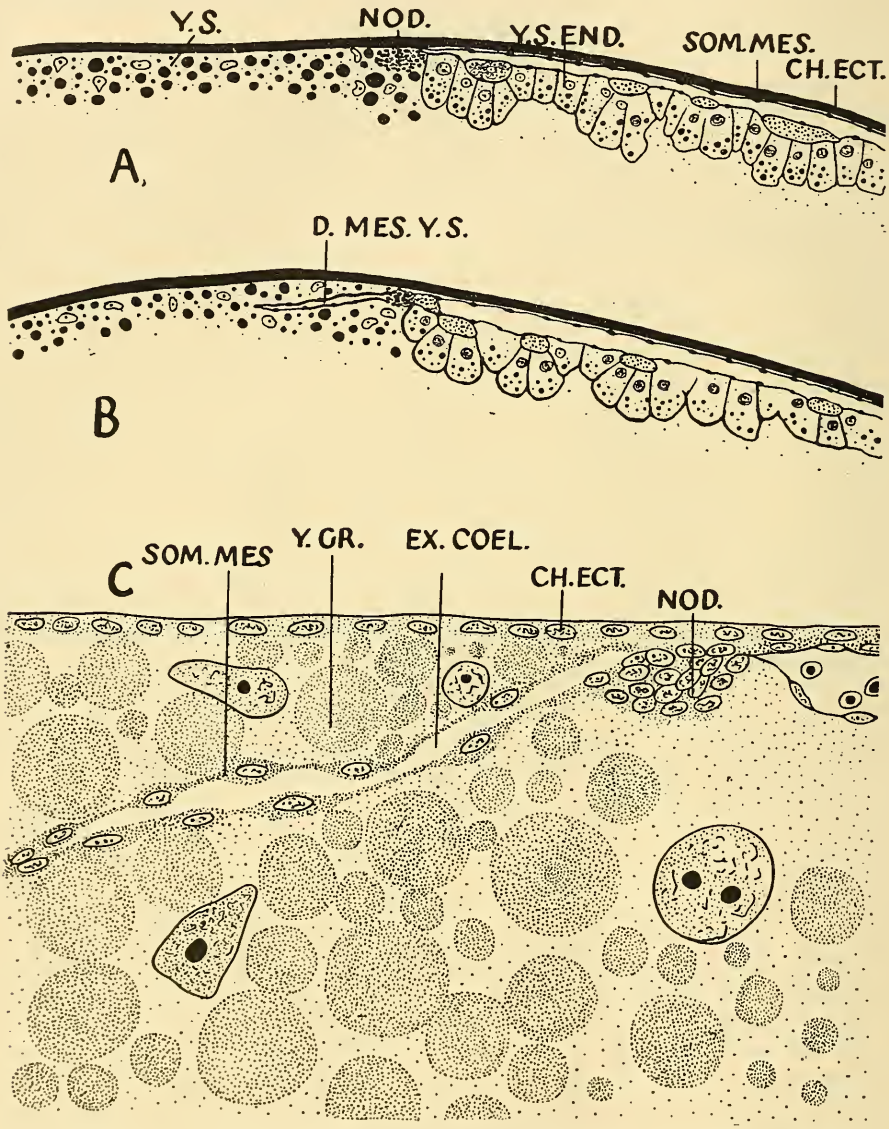
The structure of the uterine wall has changed slightly in this region. The epithelial cells have increased in length, are definite and columnar, the protoplasm at the free margins staining deeply, but they are very narrow and crowded together and have not the same regular appearance as in more advanced stages in the development of the omphaloplacenta.

The layer of endoderm underlying the area vasculosa on the dorsal surface of the sac differs from the rest, consisting of large columnar cells, each with a definite boundary and with its base rounded and buried in the yolk. The cells are vacuolated and contain large nuclei and many small yolk granules (Text-fig. 6, Y. S. END.). This layer of endoderm is homologous with that underlying the area vasculosa in chick embryos (Lille, p. 129). The boundaries of the endoderm cells filling the rest of the yolk-sac are difficult to determine, their cytoplasm being full of yolk granules and large vacuoles. It will be recalled that the yolk-sac endoderm is closely attached to the overlying chorionic ectoderm, and this close attachment plays an important part in determining the structure of the omphaloplacenta by bringing about the modification in the growth of the extra-embryonic mesoderm as mentioned above. The growth is normal up to a certain stage, the sinus terminalis being arrested for a short time at the junction of the chorionic ectoderm and the yolk-sac endoderm. The area vasculosa under these conditions measures on an average 7 mm. and consists of two main vitelline arteries and veins. But the period of quiescence in the growth of the mesoderm is short and the omphaloplacenta does not function for long in a non-vascularized condition. The mesoderm cells at the circumference of the area vasculosa divide fairly rapidly, but so close is the connection between the yolk-sac endoderm and the chorionic ectoderm that the cells cannot force their way between them, and consequently their progress is delayed and a thick margin of mesoderm cells is formed surrounding the area vasculosa, which in transverse section has the appearance of a rounded nodule of small dark cells (Text-fig. 6, A, NOD.). Since there is no longer a passage for the extension of the mesoderm between the ectoderm and endoderm it is forced to dip into the yolk-sac and continue its growth round the yolk-sac, not over its surface as is usually the case, but embedded in its substance (Text-fig. 6, B and C; Pl. xxxviii, fig. 2).

As the mesoderm pushes into the yolk-sac endoderm it splits into somato-pleural and splanchnopleural layers as it does in the normal condition when forming the extra-embryonic coelome, and thus separates an outer layer of endoderm from the main bulk of the yolk-sac endoderm. This outer layer is fairly regular in width at the sides of the yolk-sac, measuring approximately 0·075 mm. in some embryos. However, at the base of the yolk-sac in the region of the persistent area of modified ectoderm and endoderm, the mesoderm may grow up into the yolk-sac for a considerable distance and so cut off an outer layer of endoderm measuring as much as 0·210 mm. in width. At this stage (one week after fertilization) the mesoderm has commenced to dip into the yolk-sac for the short distance of 0·615 mm. and the area vasculosa still measures approximately 7 mm., there being no sign of haematopoiesis in the mesoderm within the yolk-sac (Text-fig. 6, C). Since the mesoderm does not entirely surround the yolk-sac until the embryo is at least four weeks old, the vascularization of the yolk-sac is not completed until then and will be described at Stage B.

The Allantoplacenta.—Although the development of an allantois of sufficient extent to lie immediately under the chorion is necessary for the formation of the allantoplacenta, the maternal wall becomes modified in anticipation of placentation

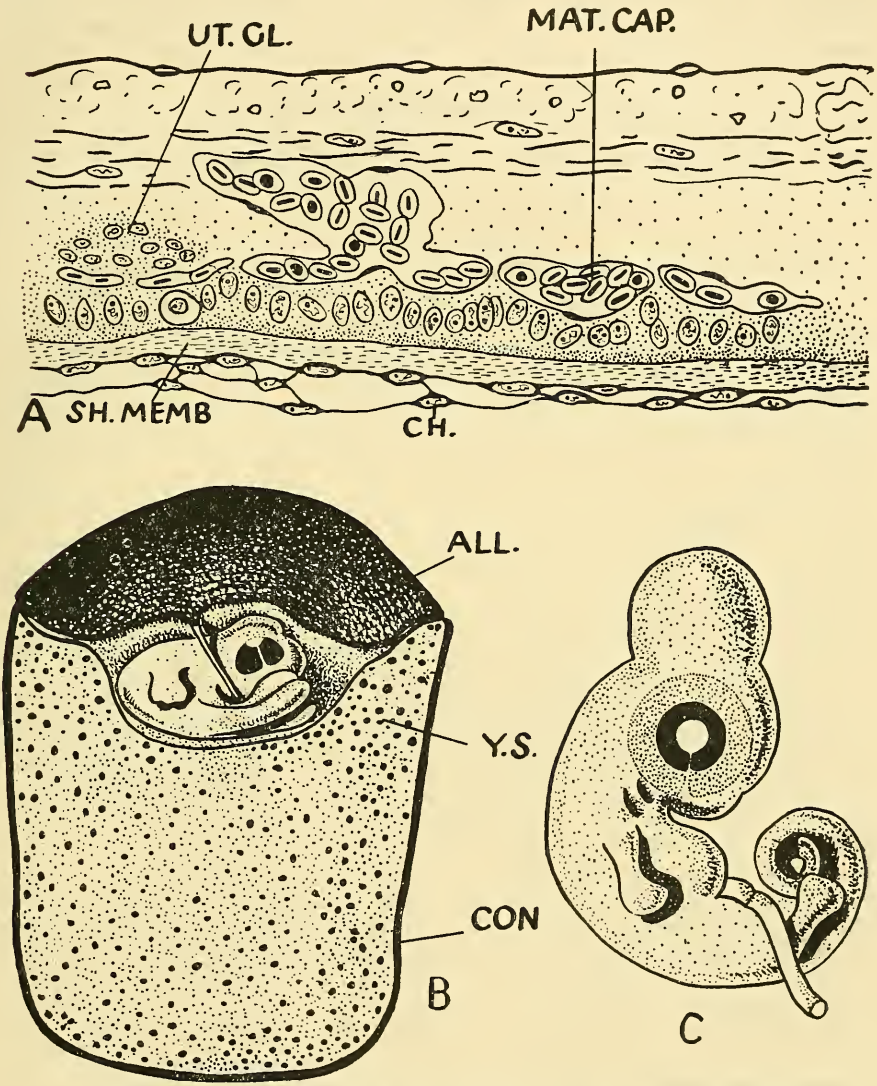
when the embryo is a week old (Text-fig. 7, A), at the time when the allantois is but a small swelling at the posterior end of the embryo and the omphaloplacenta first begins to function. It is not until the embryo is approximately two weeks



Text-fig. 6. A, section of the yolk-sac at the edge of the area vasculosa showing the formation of the nodule of mesoderm; × 159. B, section of yolk-sac of an older embryo showing the downgrowth of the mesoderm into the sac; × 159. C, the same, under higher power; × 511. CH. ECT., chorionic ectoderm; D. MES. Y. S., downgrowth of mesoderm into the yolk-sac; EX. COEL., extra-embryonic coelome; NOD., nodule; SOM. MES., somatic mesoderm; Y.S., yolk-sac; Y.S. END., yolk-sac endoderm; Y. GR., yolk granule.

old that the chorio-allantoic membrane is formed and the allantoplacenta established.

At a stage a week after fertilization the amniotic folds have met above the embryo to complete the chorionic membrane and it is in this region that the uterine wall is first modified. The modification is brought about by the multiplica-



Text-fig. 7. A, section showing the modification in the maternal wall before the formation of the chorio-allantoic membrane; × 560. B, section through the blastocyst at the end of the second week when the chorio-allantoic membrane is first formed; × 8·5. C, the embryo at this stage; × 13. ALL., allantois; CH., chorion; CON., constriction; MAT. CAP., maternal capillary; SH. MEMB., shell membrane; UT. GL., uterine gland; Y.S., yolk-sac.

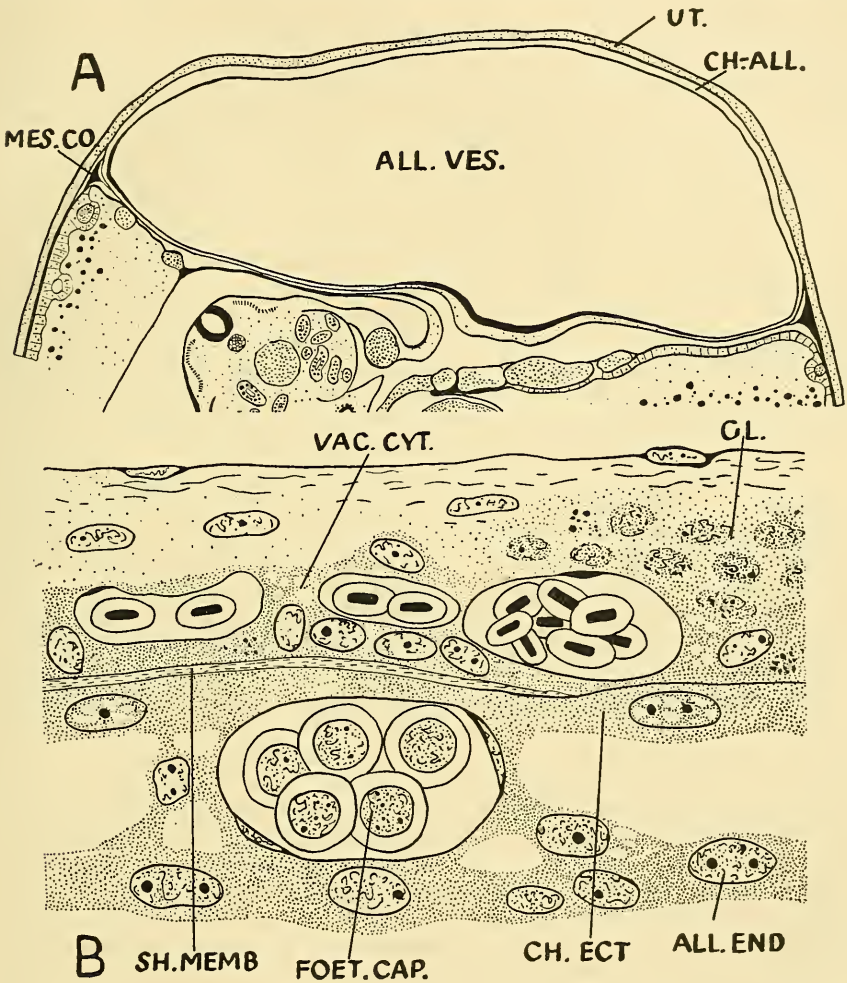
tion and expansion of a few of the maternal capillaries present in the mucosa between the saccular glands and the epithelium, and by their attempt to invade the overlying epithelium (Text-fig. 7, A). The invasion of the epithelium by the capillaries has not advanced far, the epithelium being intact over the surface of the uterus with no breaks in its continuity such as occur at the stage of placental maturity. It will be recalled that the epithelium lining the incubatory chambers is a single layer of fairly large columnar cells. The pressure on these cells in the region of the invading capillaries causes them to become flattened, so that they now measure about 0·016 mm., one-third of their original height. The compression of the cells is followed by their degeneration, which is most marked in later stages, the compressed cells at this stage retaining their individuality although their cytoplasm may be slightly vacuolated. Since the embryo is but a week old the shell membrane between the uterine epithelium and the chorionic membrane is practically unchanged, although the chorionic ectoderm cells have attacked it and are embedded in its substance. The chorionic membrane is normal in structure, the ectoderm cells being small, flat and unmodified. The growth of the allantoic vesicle and the formation of the chorio-allantoic membrane occur during the following week, so that, when the embryo is two weeks old (Text-fig. 7, B) the main requisites for the formation of an allantoplacenta are first acquired, there being a uterine wall in close proximity to a well vascularized chorio-allantoic membrane. The blastocyst from the coastal type of female containing a two weeks old embryo measures approximately 1·3 cm. × 0·9 cm., and the contained embryo 0·6 cm., but its body is so curved, the head and tail almost meeting, that it is impossible to give exact measurements, the length given being the crown-rump measurement. The head is large, the eyes are prominent, and the limb buds present, the stage in development roughly approximating that of a four-day-old chick embryo (Text-fig. 7, C). The embryo lies on its left side and is sunk down into the yolk-sac, the top of the sac often being level with that of the embryo (Text-fig. 7, B). The area vasculosa extends a little more than half-way round the yolk-sac and its boundary is marked by a constriction of the sac, which can be seen in the living as well as in the fixed condition (Text-fig. 7, B, CON.).

The allantoic vesicle measures approximately 0·4 cm. in diameter. As the embryo grows the vesicle expands radially until its wall meets the upper surface of the yolk-sac which automatically stops further progress, the vesicle only expanding as the yolk-sac decreases in size. As yet there is no definite, long allantoic stalk, the allantoic vesicle opening directly into the hind gut and being vascularized by two main arteries and veins.

The area of allantoplacentation is not limited, placental modifications of maternal and foetal tissues occurring over the entire area embraced by the allantois (Text-fig. 8, A). As the embryo develops, its yolk-sac is gradually absorbed and the allantoic vesicle expands filling the former position of the yolk-sac. The expansion of the allantoic vesicle and consequent radial extension of the chorio-allantoic membrane is accompanied by a corresponding extension of the placental region. It is peculiar that the uterine wall is always modified for a short distance beyond the limit of its proximity to the allantois, and is thus always prepared for the growth of the allantois and the extension of the placental region.

At this stage the uterus is distinct from the chorionic membrane even when there is no shell membrane present to divide them, the chorionic cells not having yet begun to attach themselves to the uterus.

(*a*). *Maternal Portion of the Placenta.*—The wall of the uterus is thinner in the placental than in the non-placental region due to the degeneration of the glands and muscle layers and the partial degeneration of the epithelium. The decrease in the number of glands in this region is particularly apparent when the uterus is viewed through the binocular microscope (Text-fig. 2, A). The few glands present are so compressed as to have no resemblance to their former shape, the cell nuclei being arranged in a flat ring, and the cell cytoplasm being



Text-fig. 8. A, section of the dorsal portion of a blastocyst during the third week of the gestation period, showing the extent of the allantoplacenta and the general disposition of the membranes. B, section through the allantoplacenta, stage A; × 1685. ALL. END., allantoic endoderm; ALL. VES., allantoic vesicle; CH.-ALL., chorio-allantoic membrane; CH. ECT., chorionic ectoderm; FOET. CAP., foetal capillary; GL., gland; MES. CO., mesodermal connection; SH. MEMB., shell membrane; UT., uterus; VAC. CYT., vacuolated cytoplasm.

intensely vacuolated. The degeneration of the glands is accompanied by a deposition of pigment granules.

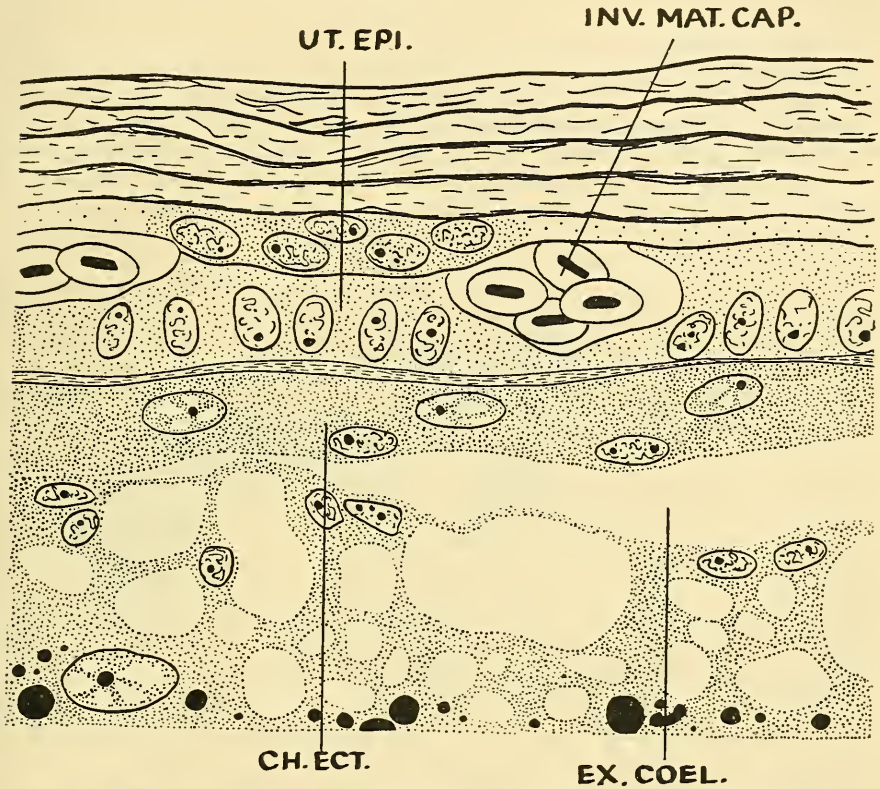
The vascularization of the uterus is richer than in the first week of pregnancy. The large vessels are situated in the mucosa overlying the glandular region and the capillaries are dispersed among the glands particularly above the epithelium. Each capillary has a distinct endothelial lining containing small dark nuclei. The capillaries are mostly small and flat and are not as numerous as at later stages. They contain a few elongated corpuscles each with a deeply staining ellipsoidal, almost rectangular nucleus. The capillaries have progressed in their invasion of the epithelium and appear to push against the overlying epithelial cells, but they have not as yet reached the surface of the uterus (Text-fig. 8, B). The degeneration of the epithelium is more marked than in earlier stages. The cell walls and many of the nuclei have disappeared and the cell cytoplasm is well vacuolated. A few healthy cells are present and each has a small oval granular nucleus.

The persistence of the shell membrane varies for different embryos, some at this stage having no membrane, some having a thin remnant, and others having quite an appreciable amount. The membrane when present is pressed between the chorion and the uterine wall, but there is a tendency for it to break away from the uterine wall and remain attached to the chorion, this being due to the absorption of the substance of the membrane by the underlying cells of the chorionic ectoderm. That the shell membrane is being absorbed by the chorionic cells is obvious, since the chorionic cells are found embedded in its substance and in stained sections the cell cytoplasm has the same appearance as the membrane; also the membrane is present in some places and not in others, and is thinner in the placental than in the non-placental region.

(*b*). *Foetal Portion of the Placenta.*—There is little modification of the chorio-allantoic membrane, possibly due to the restricting presence of the shell membrane, since the chorionic ectoderm cells must first destroy it before they can come into contact with the uterus. The chorionic ectoderm consists of a single layer of small, uniform, tapering cells with no visible dividing walls (Text-fig. 8, B). Each cell contains an oval nucleus with usually two bright nucleoli, the nuclei staining deeper than those of the uterine epithelium and hence being easily distinguished from them throughout the life of the placenta.

The chorio-allantoic membrane is well vascularized by a rich network of capillaries underlying the chorionic ectoderm. The capillaries measure 0·025 mm. in diameter, being much larger than the maternal capillaries, and are full of young corpuscles which are easily distinguished by their round shape and round nuclei from the oblong maternal corpuscles. The connective tissue in which the vessels and capillaries are carried is comparatively thick, consisting of a network of young tapering cells, there being as yet no muscle fibres present among them. There is a single bounding layer of allantoic endoderm, the cells of which resemble those of the connective tissue. The restrictions to the efficient functioning of the allantoplacenta are the presence of the shell membrane and the absence of any modification of foetal tissue in the placental region. However it is evident that a certain amount of maternal secretion is being absorbed by the foetal tissue, since in this region there is none of the secretion from the compressed glands in the mucosa such as is present in the non-placental area, described below. That the chorionic ectoderm cells are ingesting is shown by their absorption of the shell membrane and it is probable that at the same time they receive maternal materials through it.

The maternal portion of the placenta at this stage, then, is represented by a general thinning of the uterine wall due to a partial degeneration of the muscle layers and glands; by increased vascularization; by the invasion of the uterine epithelium by the overlying capillaries and by the consequent compression, flattening and degeneration of the epithelial cells. The foetal portion of the placenta consists of a thin chorion attacking and absorbing the shell membrane and overlying a well vascularized allantois.



Text-fig. 9. Section of the region of partial maternal placentation; × 1685. CH. ECT., chorionic ectoderm; EX. COEL., extra-embryonic coelome; INV. MAT. CAP., invading maternal capillary; UT. EPI., uterine epithelium.

(*c*). *Region of Partial Maternal Placentation.*—It will be recalled that the uterine wall overlying the yolk-sac at the edge of the allantoplacental area is influenced for some distance by allantoplacentation and is modified accordingly (Text-fig. 9). Here the uterine wall is thicker than in the placental region and the glands although still flattened are more prominent. The secretion which is forced from these glands on the stretching of the uterus is present in abundance among the tissues of the mucosa (Text-fig. 9). The uterine epithelium is thick and the cells uniform, with indefinite boundaries, yet the capillaries have begun to invade them, this invasion being the main placental modification. The shell membrane is thick but is degenerating apparently through the activity of the

underlying chorionic ectoderm cells, which, however, are more easily separated from it here than in the allantoplacental region. The chorionic ectoderm immediately overlies the extra-embryonic mesoderm as far as the sinus terminalis, when the mesoderm dips down into the yolk-sac as described, the chorionic ectoderm then being attached to the endoderm cells of the yolk-sac. That the uterine wall is secreting materials is quite possible but the presence of the glandular secretion among the tissues of the mucosa in this region and its absence in the placental region indicates the contrary.

Stage B. *The Stage of Placental Maturity.*

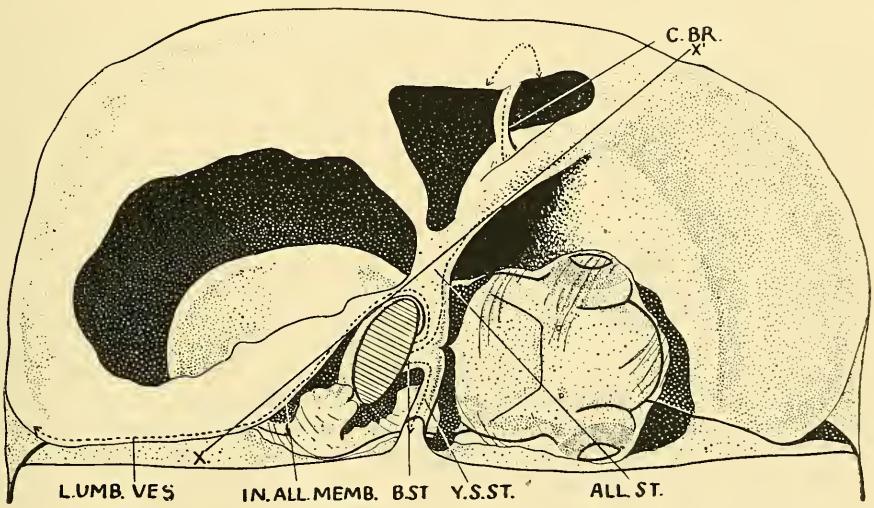
The stage of omphaloplacental and allantoplacental maturity covers the last two months of the gestation period. The mature omphaloplacenta is not uniform in structure, being more specialized in some embryos than in others and even in its most specialized form is not as well developed as that in specimens of *L. entrecasteauxi*, *T. scincoides* and *E. whitei* examined by the writer. The difference in the degree of specialization of the placenta makes it difficult to estimate the exact time of its maturity, since the placentae in embryos at the same stage in development may vary in structure, but the third week is thought to be the most probable time of omphaloplacental maturity. The mature allantoplacenta is more uniform in structure and the time of its maturity is consequently more easily ascertained. The allantoplacenta is fully specialized to function as a nutritive and respiratory organ when the embryo is between three and four weeks old, and so functions with slight alterations in histological structure over the ensuing two months prior to the birth of the foetus. The structure of the placenta of a fully formed foetus is influenced by approaching birth and will be described separately as Stage C.

Nine females containing embryos with a mature omphaloplacenta and allantoplacenta were collected from Barrington Tops at intervals during January and December, 1925; twelve from the Blue Mountains during January, 1927, and eight from Sydney during November and December, 1926. The embryos in the females collected from Barrington Tops ranged in age from four to nine weeks; those in females from the Blue Mountains from about nine to ten weeks; and those in females from Sydney from three to ten weeks.

The difference in size between the blastocyst from the mountain type of female and that from the coastal type is most noticeable, the blastocyst of the mountain type measuring on an average one-half that of the coastal type. The number of young present in each female corresponds with the figures quoted for stage A, the females from the mountain region carrying from two to five young and those from the coastal region from five to nine young. When there is only a moderate number of blastocysts within the uterus and each embryo has room to grow without interference from the others, the blastocyst is roughly oblong in shape with its long axis parallel to that of the female, and each is isolated in its incubatory chamber; but when they are crowded and pressed together their depth is as great as, if not greater than, their length. They are sometimes pressed so closely together that the uterus is no longer constricted between them to form definite incubatory chambers but remains distended so that the embryonic membranes over a small area at both ends of one blastocyst are in close proximity with those of the two adjacent blastocysts.

As in *L. entrecasteauxi* (Harrison and Weekes, 1925, p. 473) certain structures are more or less visible through the thin and much distended uterine wall, and

"as the parent lies upon her back, with the ventral body wall opened up, and the uteri exposed, the region of the yolk-sac for each embryo shows as a creamy area, ventral and lateral, *i.e.*, anti-mesometrial in position". The placentae of embryos obtained from females during the fourth week of the gestation period are selected for description and such variations as are found in the placentae of embryos at later stages will be described separately. When the four weeks old blastocyst is examined ventrally, although the yolk-sac has been absorbed from the immediate region of the embryo and reduced to half its original size, it obscures from view most of the underlying embryo, which is only completely visible when the blastocyst is turned round. The embryo can then be seen lying on its left side on the yolk-sac with its body curved so that head and tail meet, and with the tail coiled round the limbs. The vascularization of the uterine wall, allantoic vesicle and yolk-sac can be clearly seen. Beyond a general enlargement of the vessels in the uterine wall the maternal circulation does not differ from that described at stage A, the vessels encircling each incubatory chamber as far as the base of the yolk-sac.



Text-fig. 10. Four weeks old embryo lying upon the yolk-sac, showing the general disposition of the foetal membranes; × 7·5. ALL. ST., allantoic stalk; B. ST., body stalk; C. BR., cellular bridge; IN. ALL. MEMB., inner allantoic membrane; L. UMB. VES., left umbilical vessels; Y. S. ST., yolk-sac stalk.

The embryo at this stage (Text-fig. 10) is closely wrapped in the amnion and is a uniform white colour, there being no scale marking nor any indication of scales in sectioned material. The head is large, the eyes prominent, the nasal apertures formed, and the mouth distinct with upper and lower jaws, tongue and rudimentary teeth forming. The joints and digits of the fore and hind limbs are fairly well developed. The body stalk leaves the posterior end of the embryo in the region of the hind limbs and soon separates into yolk-sac and allantoic stalks. The yolk-sac stalk passes immediately downwards carrying the vessels connecting the vascularization of the yolk-sac with that of the embryo. The allantoic stalk passes up and round the embryo expanding into the allantoic vesicle which

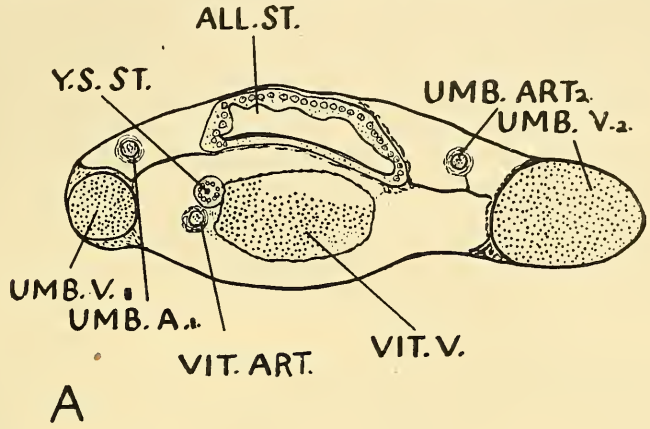
measures approximately 5 mm. if the embryo is from a female of the mountain type and 13 mm. if from one of the coastal type. As in earlier stages the allantois does not surround the yolk-sac and only expands in a downward direction as the yolk-sac decreases in size.

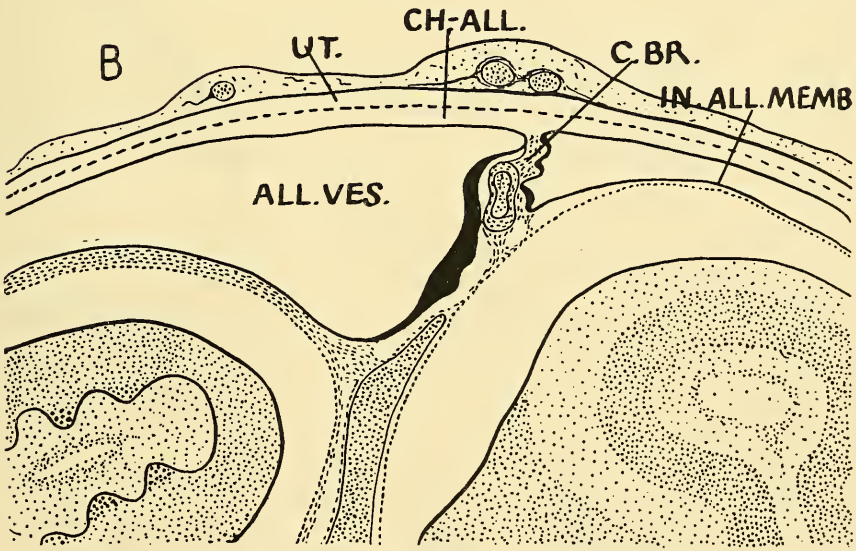
In the body stalk the allantoic stalk has the appearance of being folded round the yolk-sac stalk, owing to the presence of allantoic vessels on either side of the embryo, while the yolk-sac receives vessels from one side only. The yolk-sac stalk is narrow in comparison with the allantoic stalk and its cavity has almost disappeared, being lined with fairly large columnar cells (Text-fig. 11, A). The cavity of the allantoic stalk is much larger and is also lined with large regular cells. The yolk-sac stalk enters the gut immediately anterior to the allantoic stalk. The various bloodvessels are slung in thick folds of mesenchyme arranged round the two stalks, the mesenchyme of both stalks intermingling. There are two umbilical arteries and two veins arranged round the cavity of the allantoic stalk, and one vitelline artery and one vein round the cavity of the yolk-sac stalk. In Text-fig. 11, A, the relationship between the allantoic and yolk-sac stalks within the body stalk is shown.

Within the body of the embryo the vitelline artery is given off by the main dorsal aorta, and the vitelline vein enters the liver. Each umbilical artery is a separate branch from the dorsal aorta in the region of the sciatic artery. As the umbilical veins enter the embryo they unite and pass to the liver where they join the intra-hepatic vessels and the ductus venosus and so pass to the heart. The vitelline artery and vein branch over the flat upper surface of the yolk-sac, at the edge of which they dip into its substance (as described at Stage A), and so completely encircle the sac. The upper surface of the yolk-sac is covered with a layer of large compact endoderm cells (described at Stage A) into which the vessels sink until they lie in deep grooves. The cells lining the grooves prevent the vessels from penetrating into the interior of the yolk-sac and it is not until the vessels have passed beyond the region of these cells and have reached the sides of the yolk-sac that penetration of the interior is possible. It is curious that the interior of the yolk-sac is vascularized by the vessels from the sides and base of the sac and never by branches of those on its upper surface. However, the large endoderm cells are thought to be probable yolk absorbers, since they retain their characteristic appearance throughout the life of the yolk-sac and are always packed with minute yolk granules.

The area vasculosa extends right round the yolk-sac and so the extra-embryonic coelome is completed. It will be seen at once that the position of the coelome is abnormal, since it actually lies within the yolk-sac, and the somato-pleure is formed from mesoderm, endoderm and ectoderm instead of from the normal layers of mesoderm and ectoderm. At the edge of the yolk-sac the somato-pleural mesoderm lining the chorionic ectoderm remains attached over a short distance to that of the splanchnopleure of the yolk-sac, and the mesoderm of the allantois joins this mesenchyme connection, so that the extra-embryonic coelome is divided into two parts, one lying in the embryonic region between the chorionic membrane and the amnion and being almost completely filled by the allantoic vesicle, and the other lying within the yolk-sac. The attachment of the allantois to the chorionic and yolk-sac mesoderm in this region was detected when the embryonic membranes were dissected away from the embryo under the binocular microscope and was puzzling until sections were made which showed its nature. The blood is collected from the chorio-allantoic membrane by the two large

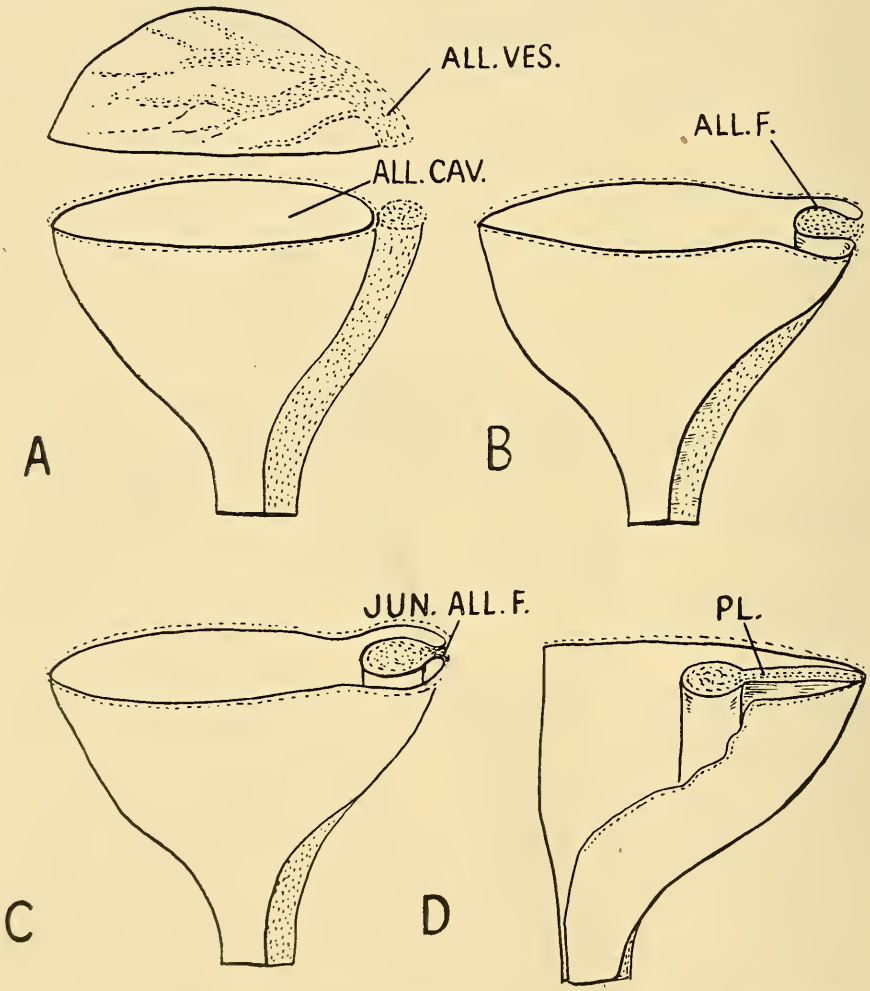
umbilical veins one of which passes around the inner allantoic wall and thence to the allantoic stalk; the other, invested by allantoic mesoderm and endoderm, reaches the allantoic stalk by passing directly across the cavity of the allantoic





Text-fig. 11. A, section of the body stalk showing the general relationship between the allantoic and yolk-sac stalks; × 86. B, section of the allantoic vesicle in the region of the vascular bridge; × 16·5. ALL. ST., allantoic stalk; ALL. VES., allantoic vesicle; C. BR., cellular bridge; CH. ALL., chorio-allantoic membrane; IN. ALL. MEMB., inner allantoic membrane; UMB. ART., umbilical artery; UMB. V., umbilical vein; UT., uterus; VIT. ART., vitelline artery; VIT. V., vitelline vein; Y. S. ST., yolk-sac stalk.

vesicle (Text-fig. 11, B). Each of the veins is accompanied throughout its ramification in the chorio-allantoic membrane by one of the umbilical arteries. This method of transmission of blood vessels across the cavity of the vesicle is interesting but is evidently of common occurrence since it is found in embryos of some mammals and reptiles examined. Hubrecht (1889, pp. 307-8) records it for the hedgehog, Flynn (1923, p. 77, and fig. 1, p. 74) for *Tiliqua scincoides*, and Harrison and Weekes (1925, p. 476) for *L. entrecasteauxi*. For the hedgehog Hubrecht (1889, pp. 307-8) described "cellular bridges" which crossed the allantoic cavity to carry blood vessels from the inner to the outer allantoic membrane. Flynn wrote, "But the outer wall of the vesicle is also supplied by vessels which leave the allantoic stalk near the body of the embryo and pass right across



Text-fig. 12. Diagrammatic representation of the formation of the vascular bridges across the allantoic cavity. ALL. CAV., allantoic cavity; ALL. F., allantoic fold; ALL. VES., allantoic vessels; JUN. ALL. F., junction of allantoic folds; PL., pleat.

the vesicle to ramify through the mesenchymal layer of the placental face of the allantois". Harrison and Weekes (p. 476) described a somewhat different method of transmission for *L. entrecasteauxi* where "a pleated fold arises from the inner allantoic wall (Plates xlvii, fig. 3; xlviii, fig. 2; xlix, fig. 5, Pl.), within the inner free edge of which the vessels are carried. Since this pleat is covered externally with endoderm continuous with that lining the allantois, there would appear to be no doubt that it has arisen originally as a fold of the allantoic wall". The authors also noted that "In our fourth series a somewhat different condition occurs. In place of the flat fold a blunt finger-like process is pushed out from the inner wall and passes across the lumen to bring about the same ultimate result".

An examination of the various available early stages in the development of *L. quoyi* reveals the suprisingly simple method of the formation of the bridges across the allantoic cavity and indicates a similarity between the methods of transmission in *L. quoyi*, *L. entrecasteauxi* and *T. scincoides* and possibly in the hedgehog.

The position of the blood vessels in the allantoic vesicle in *L. quoyi* is due to the comparatively rapidly growing wall of the vesicle enfolding the more slowly growing blood vessels present in its mesenchyme (Text-fig. 12B, ALL. F.). The arms of the folds from either side meet (Text-fig. 12, C), and thus separate the vessels from the rest of the vesicle wall except for a pleat-like connection which may remain helping to hold the suspended vessels in position (Text-fig. 12, D, PL.). Such a pleat may evidently persist in *L. entrecasteauxi* as quoted above, but in *L. quoyi*, in one of the four specimens of *L. entrecasteauxi* examined, and apparently in *T. scincoides*, it becomes disconnected from the main vessels which then have the appearance of being carried across the cavity in "blunt finger-like processes" pushed out from the walls of the vesicle. The enfolding of the vessels by the wall of the vesicle accounts for the presence of the coat of allantoic endoderm surrounding them, and, I think, for the substance of the "cellular bridges" in *T. scincoides* mentioned by Flynn, although he has not indicated the nature of their tissue either in the text or the accompanying figure.

Since the embryo lies on its left side, the underneath wall of the allantoic vesicle is pressed against the posterior end of the embryo and the yolk-sac and is so prevented from expanding in a downward direction; consequently the lower wall of the vesicle, which is vascularized by the left umbilical vein and artery, does not grow to the same extent, nor as rapidly, as the upper wall, and this, I think, accounts for the absence of "cellular bridges" carrying the left umbilical vein and artery across the cavity of the allantoic vesicle. The inner allantoic wall is so tenuous and so closely wrapped round the tail and hind limbs of the embryo, that in serial sections one may easily be misled into believing that the allantoic stalk passes downward and outward over the surface of the embryo. However, a glance at Text-fig. 10 will show that sections cut along the plane $x\text{-}x^1$, in the region of the left umbilical vein and artery, would have this appearance. In Text-fig. 10 the embryo is drawn lying upon the yolk-sac with the body stalk (B. ST.), leaving the posterior end of the body and dividing into the yolk-sac stalk (Y.S. ST.), and the allantoic stalk (ALL. ST.). A portion of the wall of the allantoic vesicle has been removed so that the transmission of the blood vessels across the allantoic cavity in the "cellular bridge" can be seen (C. BR.) as well as the folding of the inner allantoic membrane round the tail of the embryo (IN. ALL. MEMB.), and the consequent passage of the left umbilical

vein and artery (L. UMB. VES.), to the chorio-allantoic membrane in a groove of the inner allantoic wall.

The Omphaloplacenta.—The lack of uniformity in the degree of specialization of the omphaloplacenta in different embryos is, as stated, most probably due to the varying amount of shell membrane present underlying the yolk-sac. It will be recalled that the shell membrane falls away from the sides of the blastocyst and collects at the base of the yolk-sac between it and the uterine wall. When the wall of an incubatory chamber is cut in half round its circumference, and the lower half is gently lifted from its position underlying the yolk-sac, the remnant of the shell membrane in the form of a round flat pad of crumpled fibrous matter falls away from the base of the yolk-sac, since it is no longer supported by the uterus. The pad gradually thickens as the embryo grows and more membrane falls to the base of the yolk-sac, so that, while it is comparatively thin in the majority of embryos at four weeks, in embryos collected during the second and last month of the gestation period, it is of considerable thickness, and impresses its shape upon the overlying yolk-sac, forming a barrier between it and the uterine wall and so interfering with the modification of the foetal tissue of the omphaloplacenta. When the shell membrane is thin the foetal tissue reaches its highest degree of specialization; when it is thick in some places and thin or absent in others the modification of the foetal tissue is correspondingly patchy; and when it is abundant, as in embryos collected during the latter half of the gestation period, there is only slight modification of the foetal tissue. In *L. entrecasteauxi* (Harrison and Weekes, 1925, p. 474) there was no trace of shell membrane in any of the embryos examined, and consequently the placenta is more or less uniform in its development and is more highly specialized than that of *L. quoyi*, even at the late stage described when retrogression of its structure is suspected (p. 476).

The embryos collected during the fourth week of the gestation period have the most fully specialized omphaloplacenta (Text-fig. 13). Here, although the shell membrane completely covers the surface of the yolk-sac, it is thin and the pad at the base of the sac comparatively small.

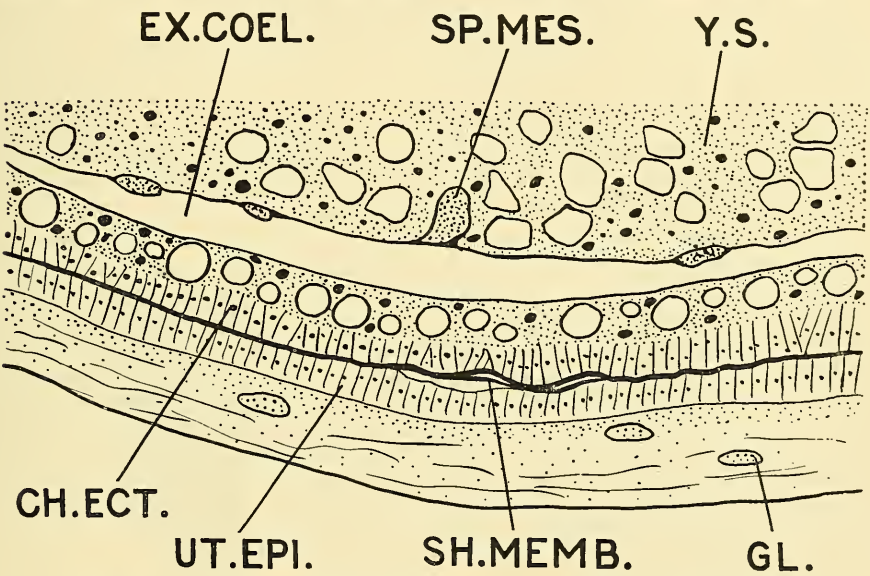
(*a*). *Maternal Portion of the Placenta.*—The maternal portion of the placenta is much less influenced by the presence of shell membrane than the foetal portion, and is comparatively uniform in structure throughout the period of omphaloplacental maturity.

There is a tendency towards a thickening of uterine tissue at the base of the yolk-sac which is fairly consistent in all embryos and especially marked in those at four weeks. The increase in thickness is brought about by a thickening of the muscular tissue and the mucosa, and by the enlargement of the epithelial cells. There is a tendency toward slight folding of the uterus, the folds being irregular and the crypts shallow. The glands in the allantoplacental region described at Stage A are conspicuous throughout the mucosa over the placental area, but although fairly numerous do not appear to function, since the cytoplasm of the gland cells is vacuolated and the cells are arranged round a large central cavity. The capillaries are numerous and mark the termination of the uterine vessels which pass round the incubatory chamber (Text-fig. 2, A). They are flat, but not as flat as in earlier stages (Text-fig. 5, B), and often bulge beneath the epithelium as in *L. entrecasteauxi*. The thickening of the uterus restores to it something of its appearance in the non-pregnant condition, but signs of placentation are present in the increased vascularization and the modified epithelium. The epithelium is formed of fairly large columnar cells with oval nuclei and with

the cell cytoplasm concentrated at their rounded free margins, this concentration being probably due to the secretory activity of the cells, since a coagulum is found adhering to many of them.

In some embryos at various stages in development the connections between the incubatory chambers are so deeply convoluted that when met with in sectioned material the uterine wall in these regions appears to be thrown into deep regular folds, which may be at first thought to be a placental modification.

(*b*). *The Foetal Portion of the Placenta.*—The modification of the foetal tissue extends over the entire under surface of the yolk-sac in proximity with the uterine wall by the radial extension of the original area of modified tissue at the approximate middle of the base of the yolk-sac. At this stage the chorionic ectoderm is thickest at the base of the sac and is composed of two or three layers of cells. The lower layers of the ectoderm are flat and squamose, and the difference between the outermost layer of cells and the underneath layers is



Text-fig. 13. Section of the mature omphaloplacenta; × 103. CH. ECT., chorionic ectoderm; EX. COEL., extra-embryonic coelome; GL., gland; SH. MEMB., shell membrane; SP. MES., splanchnic mesoderm; UT. EPI., uterine epithelium; Y.S., yolk-sac.

marked, the cells of the outer layer being tall and narrow with many of the individual cell boundaries distinct. Although the majority of the cells are columnar others may be crowded together until they have no definite shape. At the sides of the yolk-sac the ectoderm is thinner and the cells of the outer layer are smaller. There is a comparatively thin layer of shell membrane adhering to the chorionic ectoderm over the placental face but it is being absorbed by the cells and has no apparent influence on their development.

The yolk-sac endoderm underlying the chorionic ectoderm contains yolk-granules and is composed of large, vacuolated cells with large deeply staining nuclei. It is not so intimately attached to the chorionic ectoderm as in earlier

stages and the degree of attachment varies with the embryo. The boundaries of the cells are not definite, and it is impossible to estimate the number of cells in the depth of the layer. The endoderm cells are bounded by a layer of non-vascularized extra-embryonic mesoderm.

The chorionic ectoderm, together with the underlying yolk-sac endoderm and extra-embryonic mesoderm, is separated from the main bulk of the yolk-sac, with the exception of a small area at the approximate middle of the base of the sac where the mesoderm remains attached to that lining the sac.

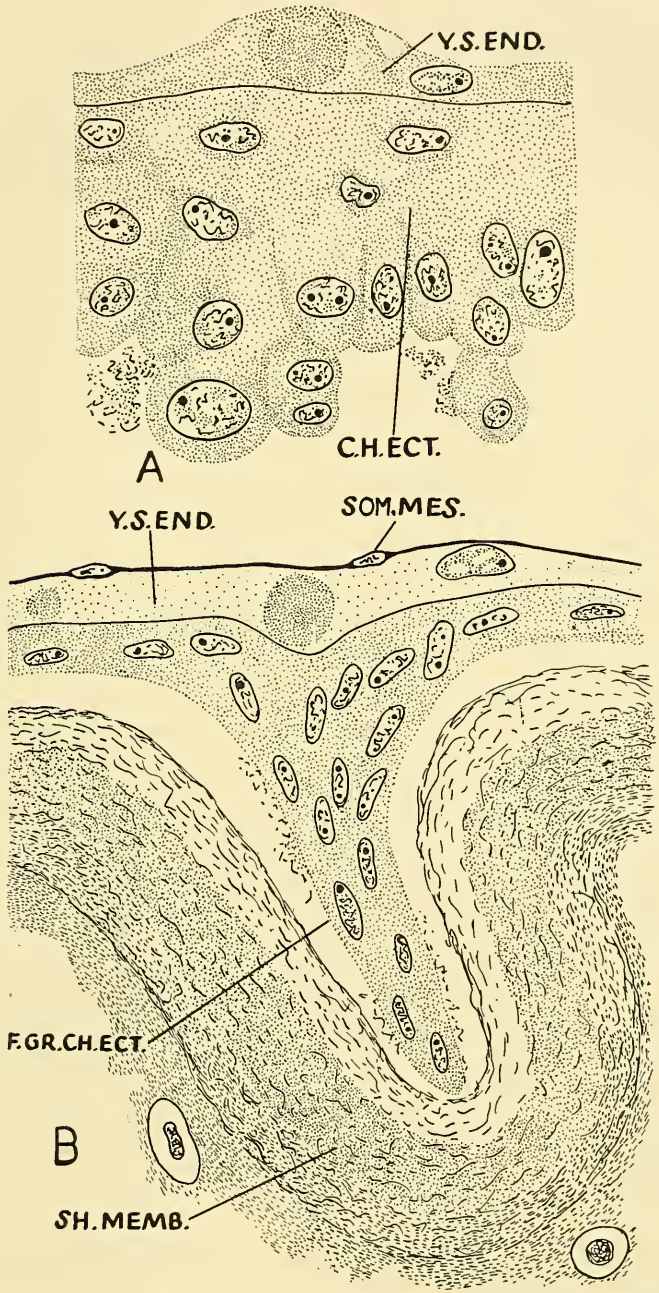
The maternal secretion absorbed by the chorionic ectoderm must be passed through the narrow layer of yolk-sac endoderm and somatopleural mesoderm and across the cavity of the extra-embryonic coelome before it reaches the blood vessels in the yolk-sac. Hence the fine coagulum within the extra-embryonic coelome, which contains corpuscles and cell debris, is thought to be maternal secretion.

The omphaloplacenta, then, present in embryos four weeks old is fairly well developed and is formed by a richly vascular uterine wall with epithelium modified for secretion overlying a many layered sheet of modified chorionic ectoderm cells, attached to a thick layer of large vacuolated endoderm cells followed by a layer of non-vascular mesoderm; the sheet of combined foetal tissue being separated by a narrow extra-embryonic coelome from the vascular system of the yolk-sac. The extra-embryonic coelome is completely cut off from the rest of the coelome in the embryonic region by a mesenchymal connection between the allantois, chorion and yolk-sac.

In embryos obtained from females collected during the sixth and subsequent weeks of the gestation period, the omphaloplacenta is not so well specialized. The maternal placenta in these corresponds with that described above and needs no further comment. During the sixth and seventh weeks, when there is a patchy accumulation of shell membrane at the base of the yolk-sac, some areas of foetal tissue are more specialized than others, the foetal placenta in the embryo selected for description being roughly divisible into two regions of varied specialization. The first region covers about one-half of the yolk-sac extending from the edge of the sac to its base and consists of practically unmodified foetal tissue underlain by a convoluted layer of shell membrane. The second region covers the rest of the yolk-sac, and as there is very little shell membrane here, the foetal tissue is well modified, the chorionic ectoderm cells attaining a height of 0·087 mm. (Text-fig. 14, A).

The chorionic ectoderm in the first region consists of two or three layers of cells which are small and flat with no dividing walls visible. The cell cytoplasm stains a deep pink with eosin and the nuclei stand out as oval darkly stained bodies. The free margins of the cells are irregular, since the cells are embedded in the shell membrane which is surrounded and impregnated by a thick coagulum thought to be maternal secretion.

The cells of the chorionic ectoderm in the second region are arranged in many layers, those of the outermost layer ranging from short, wide, cubical cells to tall, narrow, irregularly shaped cells with a tendency to columnar structure (Text-fig. 14, A). These enlarged cells are phagocytic and have ingested material, often uterine epithelial cells and maternal corpuscles, in their cytoplasm. Between the uterine wall and the chorionic ectoderm there is the same pale staining coagulum which occurs in the first region and which adheres to the edge of the chorionic cells giving them a ragged appearance. This coagulum contains the



Text-fig. 14. A, section of the foetal tissue of the omphaloplacenta of a six weeks old embryo showing the irregularly shaped chorionic ectoderm cells; × 1050. B, "finger-like" downgrowth of chorionic ectoderm in the omphalo-placental region of an eight weeks old embryo; × 1050. CH. ECT., chorionic ectoderm; F. GR. CH. ECT., finger-like growth of chorionic ectoderm; SH. MEMB., shell membrane; SOM. MES., somatic mesoderm; Y.S. END., yolk-sac endoderm.

scattered cells and corpuscles which the chorionic ectoderm cells ingest. The underlying layer of yolk-sac endoderm is thinner than in the placenta of the four weeks old embryo, the narrow cells tapering and occasionally bulging round relatively enormous yolk granules. The extra-embryonic coelome is wide and in some of the embryos examined is filled with a coagulum which is stained a deep blue by haematoxylin and which in patches has a peculiar scale-like appearance. It is full of corpuscles and has a fine granular matrix at its edges, which has the appearance of congealed blood. It is not known whether the corpuscles are maternal or foetal but both varieties are possibly present. Its occurrence between the uterine wall and the chorionic ectoderm, within the yolk-sac and within the allantoic vesicle as well as within the extra-embryonic coelome makes the problem of its origin a difficult one. A similar coagulum was observed in the yolk-sac of *L. entrecasteauxi* (Harrison and Weekes, 1925, Pl. xlviii, fig. 5) and in *E. whitei*. It was at first thought to be albumen, but this is not likely as it was not present in young embryos examined nor in the majority of older ones. Some of it is probably maternal secretion but it is not likely that this is the sole source since there is such a large quantity of coagulum present. Owing to its blood-like appearance it was thought that its presence may be due to the breaking of vessels damaged when the parent lizard was caught (Pl. xxxix, fig. 3).

In embryos present in females collected during the last month of the gestation period, the pad of shell membrane practically covers the under-surface of the yolk-sac, and there is consequently only slight specialization of the foetal tissues. For a considerable distance on either side of the yolk-sac the chorionic ectoderm cells are normal, each being flattened and having a small dark nucleus. In the central region where the shell membrane is thrown into deep folds the chorionic ectoderm is formed of many layers of small cells. These cells proliferate and grow down between the folds of the shell membrane in the form of long "finger-like" growths which may measure as much as 0·25 mm. in length and which are usually about three or four cells thick (Text-fig. 14, B). The hollows between the folds of the shell membrane on the side nearest the uterus are full of a thick coagulum which contains corpuscles and which stains pink in some places and a deep blue in others (eosin and haematoxylin). It is most probably maternal secretion and is thought to supply the stimulus for the down-growth of the chorionic ectoderm into the folds of the shell membrane. The cytoplasm of the cells of the proliferated areas has the same dense pink and blue appearance as the coagulum which the cells are obviously absorbing. Over a small area at the edge of the yolk-sac where the shell membrane is not folded but is flat and comparatively thin, the chorionic ectoderm cells are much larger and resemble the cubical chorionic ectoderm cells in the omphaloplacental region in the six weeks old embryo.

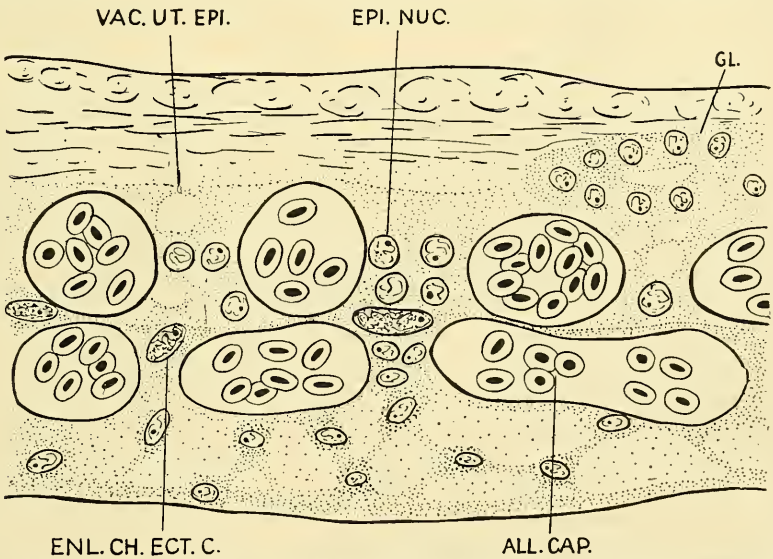
The underlying layer of yolk-sac endoderm has the same general structure as in the six weeks old embryo, being composed of either long tapering cells or large vacuolated cells. Often for a considerable distance at one side of the yolk-sac the chorionic ectoderm and strip of yolk-sac endoderm are attached to the yolk-sac.

The omphaloplacenta, then, functions best during the first six weeks of the gestation period when the foetal tissues are most highly specialized and the shell membrane covers the yolk-sac as a smooth layer. During the latter half of the gestation period its activity is diminished by the presence of the thick pad of shell membrane underlying the yolk-sac, which interferes with the passage

of maternal secretion from the uterus to the embryonic tissues, some of the secretion being retained among the folds of the membrane.

The Allantoplacenta.—By the end of the fourth week of the gestation period there is usually no shell membrane left and the chorio-allantoic membrane is pressed closely against the smooth face of the uterus and the fixation of the tissue is brought about by the attachment of scattered enlarged cells of the chorionic ectoderm to the uterine epithelium. In the handling and sectioning of the material, part of the foetal tissue may separate from the maternal tissue but there are always large areas of foetal tissue left attached to the uterus. The attachment though efficient is not as close as that in *Perameles* and there are no villous folds in the uterine wall to aid in fixation.

(*a*). *The Maternal Portion of the Placenta.*—The uterine wall is about three times thicker than in the allantoplacenta of a two weeks old embryo and the placenta is uniformly developed over its entirety, there being no special thickening of the uterine wall at the centre of the placental region such as occurs in the omphaloplacenta. With the thickening of the uterus the muscle layers, the mucosa and the few glands present have resumed something of their normal structure, but the glands show no signs of activity. The numerous capillaries have reached the surface of the epithelium and are now only separated from the underlying foetal tissue by their own endothelial walls and perhaps a thin layer of maternal cytoplasm (Text-fig. 15). They are crowded at the surface of the epithelium with their walls often touching, but with usually the width of their diameter apart. The capillary walls are thin but definite, with occasional small sickle shaped nuclei present in their substance. The capillaries are circular, packed with corpuscles, and are overlain by a series of larger vessels in the mucosa which are often found pressing against the underlying capillaries.



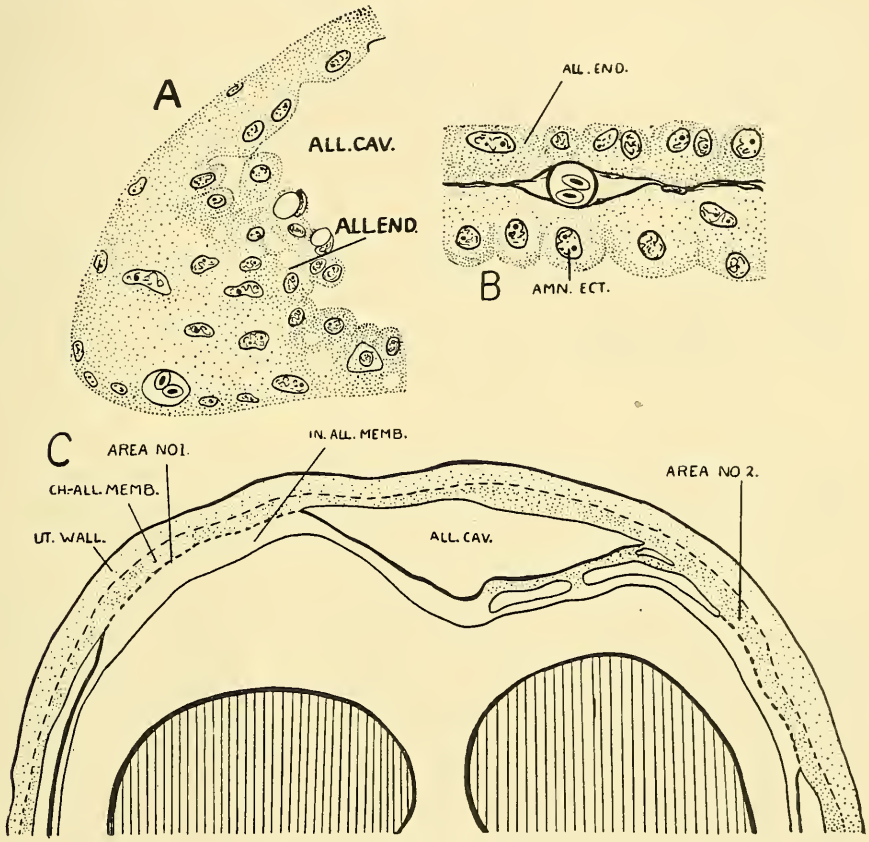
Text-fig. 15. Section of the allantoplacental region of a four weeks old embryo; × 1270. ALL. CAP., allantoic capillary; ENL. CH. ECT. C., enlarged chorionic ectoderm cell; EPI. NUC., epithelial nuclei; GL., gland; VAC. UT. EPI., vacuolated uterine epithelium.

There are few definite epithelial cells present, since most of them have degenerated, the cell cytoplasm being full of small vacuoles, the cell walls having disappeared, and a few of the degenerating nuclei being represented by groups of small dark granules. The healthy nuclei are round, stain but slightly, have one or two nucleoli, and are quite characteristic and always distinguishable from the nuclei of the chorionic ectoderm. These nuclei have been pushed aside by the invading capillaries and are now grouped in the cytoplasm between them. The cytoplasm has not the appearance of that of typical secreting cells such as are seen lining the villous ridges of *L. entrecasteauxi*, and hence is not regarded as an active secreting agent.

The absence of shell membrane allows the chorionic ectoderm and the uterine wall to come into immediate contact, but although they are attached, the connection is such that the line of division between maternal and foetal tissue is often visible, there being no mingling of the chorionic ectoderm with the maternal tissues such as occurs in the placentae of some mammals. The chorionic cells which attach themselves to the uterine epithelium are comparatively widely separated and have no definite shape, consisting of a large deeply staining nucleus surrounded by cytoplasm which insinuates processes into the maternal cytoplasm, so that when the attached maternal and foetal tissues are separated both surfaces are jagged and torn. For the rest the chorionic ectoderm consists of long tapering cells with fairly large nuclei, the tapering ends of the cells extending over the bulging allantoic capillaries or degenerating to allow the capillaries to come into immediate contact with the maternal capillaries (Text-fig. 15). It is difficult to determine whether there is more than one layer of ectoderm cells present. In some places there is a narrow gap between the maternal and foetal tissues which is filled with a coagulum staining lightly with haematoxylin, and which is possibly maternal secretion, although it may be the remains of shell membrane.

The allantoic blood vessels vary in size from small round capillaries to much larger vessels. The capillaries have distinct nucleated walls and are filled with corpuscles which closely resemble the maternal corpuscles at this stage. A narrow band of connective tissue underlies the capillaries and contains less muscle fibre than that in *L. entrecasteauxi*. The single layer of endoderm bounding the chorio-allantoic membrane consists of fairly regular, moderately enlarged tapering cells. At the edge of the placental area, where the outer wall of the allantois bends at the surface of the yolk-sac and continues as the inner wall, the endoderm cells may proliferate until they hang in bunches in the allantoic cavity (Text-fig. 16, A). Here, cell boundaries are difficult to determine, some of the cells appearing to be multinucleate. Each cell has a narrow base and a swollen apex which often contains one or more large vacuoles. The modification of the cells may extend over the inner wall of the allantois, where the cells enlarge and separate from each other at their margins (Text-fig. 16, B). They are often intensely vacuolated with a deeply staining nucleus at the surface of the cell. In the allantoplacental region of some rodents the endoderm cells have the same peculiar structure, but this modification is not a placental adaptation as is shown by a similar modification of some of the endoderm cells lining the allantoic vesicle of the oviparous Agamid lizard *Amphibolurus barbatus*. The peculiar structure of the cells is thought to be possibly caused by their absorption of the excretory fluid which fills the allantoic vesicle.

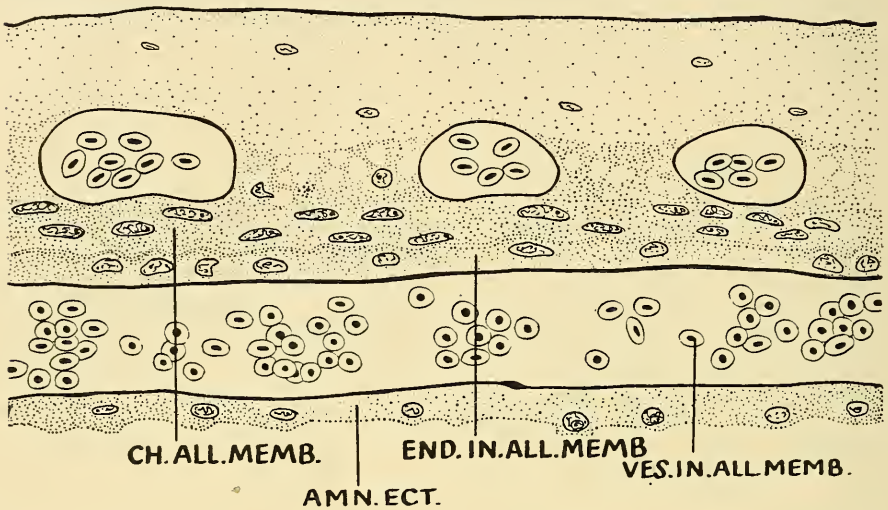
The inner allantoic membrane may unite with the amnion and the junction may extend completely over the surface of the latter, so that the blood vessels of the inner allantoic membrane come to lie between a layer of allantoic endoderm and amniotic ectoderm (Text-fig. 16, B). The ectoderm cells of the amnion are also modified, their structure resembling that of the endoderm cells just described, and this similar modification is possibly due to their absorption of excretory fluid from the endoderm cells.



Text-fig. 16. A, endoderm cells lining the allantoic vesicle at the surface of the yolk-sac; × 405. B, section showing the structure of the fused inner allantoic membrane and amnion; × 405. C, section of the allantoplacental region and allantoic vesicle showing the junction of the inner allantoic membrane and amnion with the chorio-allantoic membrane; × 17·5. ALL. CAV., allantoic cavity; ALL. END., allantoic endoderm; AMN. ECT., amniotic ectoderm; CH. ALL. MEMB., chorio-allantoic membrane; IN. ALL. MEMB., inner allantoic membrane; UT. WALL., uterine wall.

In the majority of placentae examined an interesting condition exists, where all the extra-embryonic membranes—the chorion, the outer allantoic and inner allantoic membranes, and the amnion—join together in some places to form the foetal portion of the allantoplacenta (Text-fig. 16, C; Pl. xl, fig. 7). In some

of the placentae examined the area so formed is comparatively large, measuring as much as 5 mm. in one of the embryos obtained from a mountain type of female. The presence of the additional membranes modifies the structure of the chorio-allantoic membrane in their vicinity, as described below.



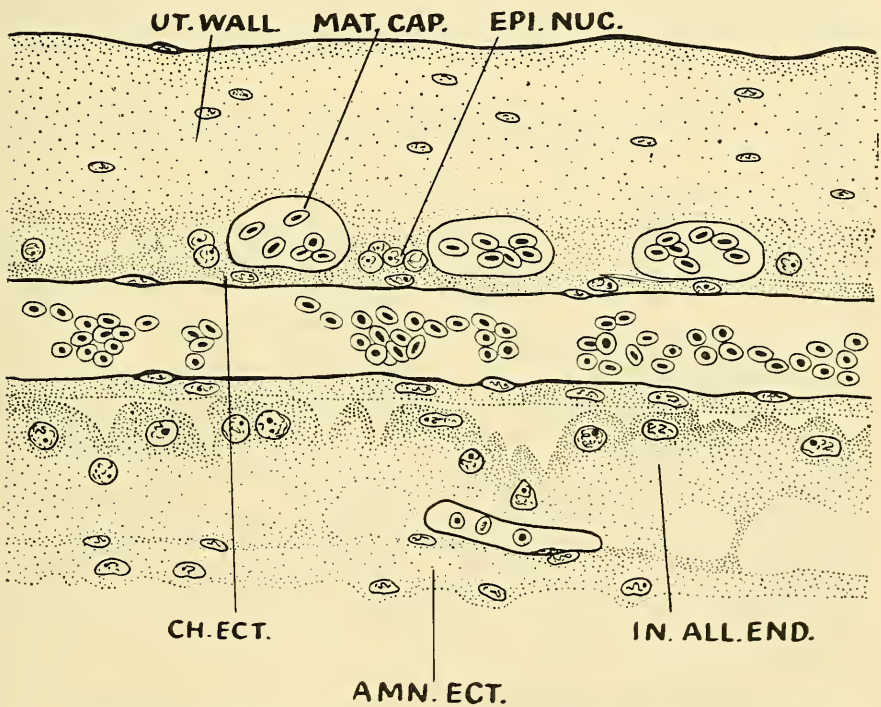
Text-fig. 17. Section of the first area of combined foetal membranes in the allantoplacental region, showing the compressed chorio-allantoic membrane and well vascularized inner allantoic wall; × 519. AMN. ECT., amniotic ectoderm; CH. ALL. MEMB., chorio-allantoic membrane; END. IN. ALL. MEMB., endoderm of inner allantoic membrane; VES. IN. ALL. MEMB., vessel in the inner allantoic membrane.

In one of the four weeks old embryos an area of combined extra-embryonic membranes is present on either side of the allantoic stalk, each of which is most conspicuous. In one of these areas the chorio-allantoic membrane is flattened against the uterine wall, and the cells of the chorionic ectoderm, mesenchyme and allantoic endoderm are so compressed that the chorio-allantoic membrane, in section, has the appearance of a narrow band of undifferentiated tissue (Text-fig. 17). One of the most obvious modifications is the absence of blood vessels in the chorio-allantoic membrane in this region (Text-fig. 17). The layer of endoderm cells lining the inner allantoic membrane is pressed closely against the chorio-allantoic membrane and there is a thin layer of coagulum between them, which fills what is left of the allantoic vesicle after the junction of its inner and outer walls, and which resembles that in the omphaloplacental region described above. The endoderm cells of the inner allantoic wall are moderately large with large oval nuclei, but have been compressed by the junction of the two membranes, until they are smaller than those in the regions of non-attachment. The underlying mesenchyme is richly vascularized and obviously feeds and drains the placenta in this region, since blood vessels are absent in the mesenchyme of the overlying chorio-allantoic membrane. The mesoderm of the amnion is joined to the mesenchyme and it and the amniotic ectoderm are normal.

On the opposite side of the allantoic stalk, the inner allantoic membrane and the attached amnion are in process of joining with the chorio-allantoic membrane

and consequently the tissues concerned here have a different structure (Text-fig. 18). The chorio-allantoic membrane is practically normal with blood vessels present in the mesenchyme. The endoderm cells of the inner allantoic membrane are greatly enlarged, measuring as much as 0·04 mm. in length, and where they touch the chorio-allantoic membrane, have attacked the substance of its endodermal lining, one of the endodermal nuclei having been torn away from its surrounding cytoplasm on the separation of the outer and inner allantoic walls in the preparation of the material for sectioning. The cells have square free margins with large vacuoles at their bases, and on the whole resemble the endoderm cells described above as lining the inner allantoic membrane in its normal position and condition. There are as yet no large blood vessels in the mesenchyme underlying the endoderm cells, but small vessels are present. The ectoderm cells of the amnion are slightly enlarged and rounded (Pl. xl, fig. 7).

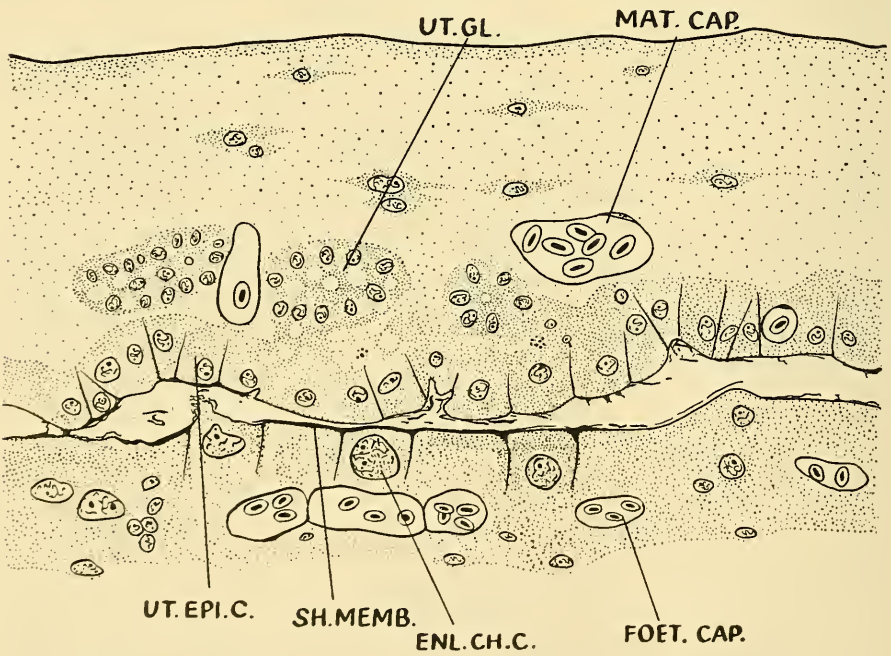
The folds of tissue which surround the blood vessels in their passage across the allantoic cavity have the same general structure as the rest of the allantoic tissue. The endoderm cells forming the outer covering of the bridges are enlarged and many layers deep, and the connective tissue is thick and muscular, carrying branch vessels as well as the main vessels across the cavity.



Text-fig. 18. Section of the second area of combined foetal membranes in the allantoplacental region showing the junction of the endodermal lining of the inner allantoic membrane with the endoderm of the chorio-allantoic membrane; × 485. AMN. ECT., amniotic ectoderm; CH. ECT., chorionic ectoderm; EPI. NUC., epithelial nuclei; IN. ALL. END., inner allantoic endoderm; MAT. CAP., maternal capillary; UT. WALL., uterine wall.

The apposition of inner and outer allantoic walls results in the formation of a short cut for the maternal secretion in its passage to the embryo. Instead of being collected by the vessels in the chorio-allantoic membrane and passed into the main right vein and thence across the cavity of the allantoic vesicle into the allantoic stalk, the secretion passes through the chorio-allantoic membrane into the vessels of the inner allantois, and thence direct to the allantoic stalk and so into the embryo. As far as can be ascertained there is no mechanical pressure upon the inner allantoic membrane which might have effected its union with the outer allantoic membrane, the embryo lying apart from the region of junction, but there is no positive evidence that the union has been caused by an urge for quicker transport of blood to the embryo. In its downward growth the inner wall of the allantois meets the amnion and the union of the two membranes is the natural result. This is established before the junction of the inner and outer allantoic membranes and so the amnion is carried to the placenta by the agency of the inner allantoic membrane, and obviously can have no new function in the placental region.

The anticipation of the extension of the allantoic vesicle by the uterine wall overlying the yolk-sac is as marked as in earlier stages. However, during the last two weeks of the gestation period when the yolk-sac is rapidly absorbed and reduced to a small bag, the allantois advances rapidly and the changes which take place in the uterus are most marked and will be described at Stage C.



Text-fig. 19. Section of the folded allantoplacental region present in one of the embryos examined; × 450. ENL. CH. C., enlarged chorionic ectoderm cell; FOET. CAP., foetal capillary; MAT. CAP., maternal capillary; SH. MEMB., shell membrane; UT. EPI. C., uterine epithelial cell; UT. GL., uterine gland.

In one of the embryos examined the allantoplacenta differs from the normal condition described above. That the variation is individual and not representative of a stage in the development of the placenta is shown by its presence in the one embryo and not in the other embryos of the same female nor in embryos of females collected at the same time, and hence approximately at the same stage in development. The embryo is about six weeks old and the allantoplacenta presents an interesting variation in the form of slight folding of the maternal and foetal tissues in the region of the main vein and artery, the folded area being 5 mm. in length and 3·5 mm. in width. The rest of the placental area is smooth as in all other embryos examined. The folds are not nearly as definite as the villous folds in the allantoplacental region of *C. tridactylus* and *L. entrecasteauxi* and in the omphaloplacental region of *T. scincoides*, and were not visible to the unaided eye. The degree of folding is shown (Text-fig. 19; Pl. xxxix, fig. 5), where the foetal tissue is seen fitting loosely into the shallow maternal crypts. The uterine wall is much thicker than in the non-folded region. The structure of the mucosa and glands is normal, but the epithelium and capillaries merit special attention. Although the epithelium of the folds has not degenerated, the cells are not as uniform in shape as in the non-pregnant condition, being crowded together in some places until they are cone shaped (Text-fig. 19). Each is slightly enlarged, has a rounded free margin and a central round or oval nucleus. The cells appear to be secretory, being non-vacuolated, and somewhat resemble those lining the villous folds of *L. entrecasteauxi*. In addition the epithelium is not interfered with to any extent by the maternal capillaries, only a few having penetrated into its substance, the remainder lying in the mucosa beneath the epithelium. However the whole area is not as well vascularized as the non-folded region.

Between the maternal and foetal tissues there is a thin remnant of shell membrane extending over the whole of the placental area. The chorionic ectoderm cells have not degenerated to the same extent as they have in the non-folded region and some are larger here than in any other of the allantoplacentae examined, but the majority are normal in size and have no dividing walls or definite shape. Each cell contains a large oval or round deeply staining nucleus, which has one or two nucleoli, and which in some cases almost completely fills the cell. The foetal capillaries are numerous, the connective tissue is comparatively thick, and the structure of the endoderm corresponds to that in a normal placenta.

In the non-folded region the maternal capillaries are numerous and have reached the surface of the epithelium which for considerable stretches has completely degenerated. The allantoic capillaries have also reached the surface of the foetal tissue, the chorionic ectoderm cells being few and scattered.

In the allantoplacenta of each of the embryos collected during the last month of the gestation period the main differences from the placenta described as typically mature are (*a*) an increase and enlargement of the maternal and foetal capillaries to meet the increasing demands of the rapidly growing embryo; (*b*) the further degeneration of the uterine epithelium between the maternal capillaries; (*c*) pronounced bulging of the maternal and foetal capillaries over the placental face, the capillaries being closely apposed often with no maternal or foetal cytoplasm between them, and with their own walls reduced in thickness.

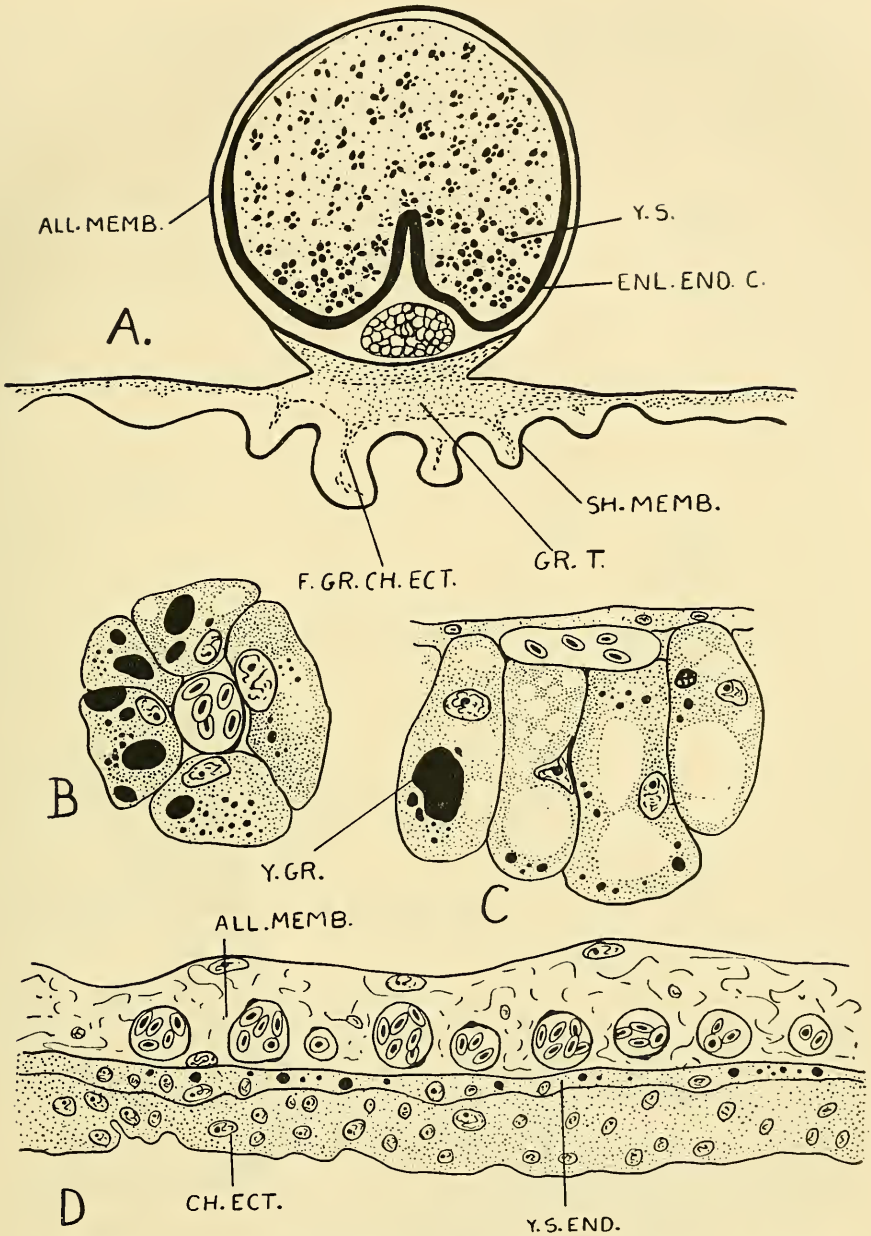
Stage C. *The placentae immediately prior to the birth of the foetus.*

Females were collected from Barrington Tops, the Blue Mountains and Kiama (coast) which contained young ranging from within two weeks to one day of

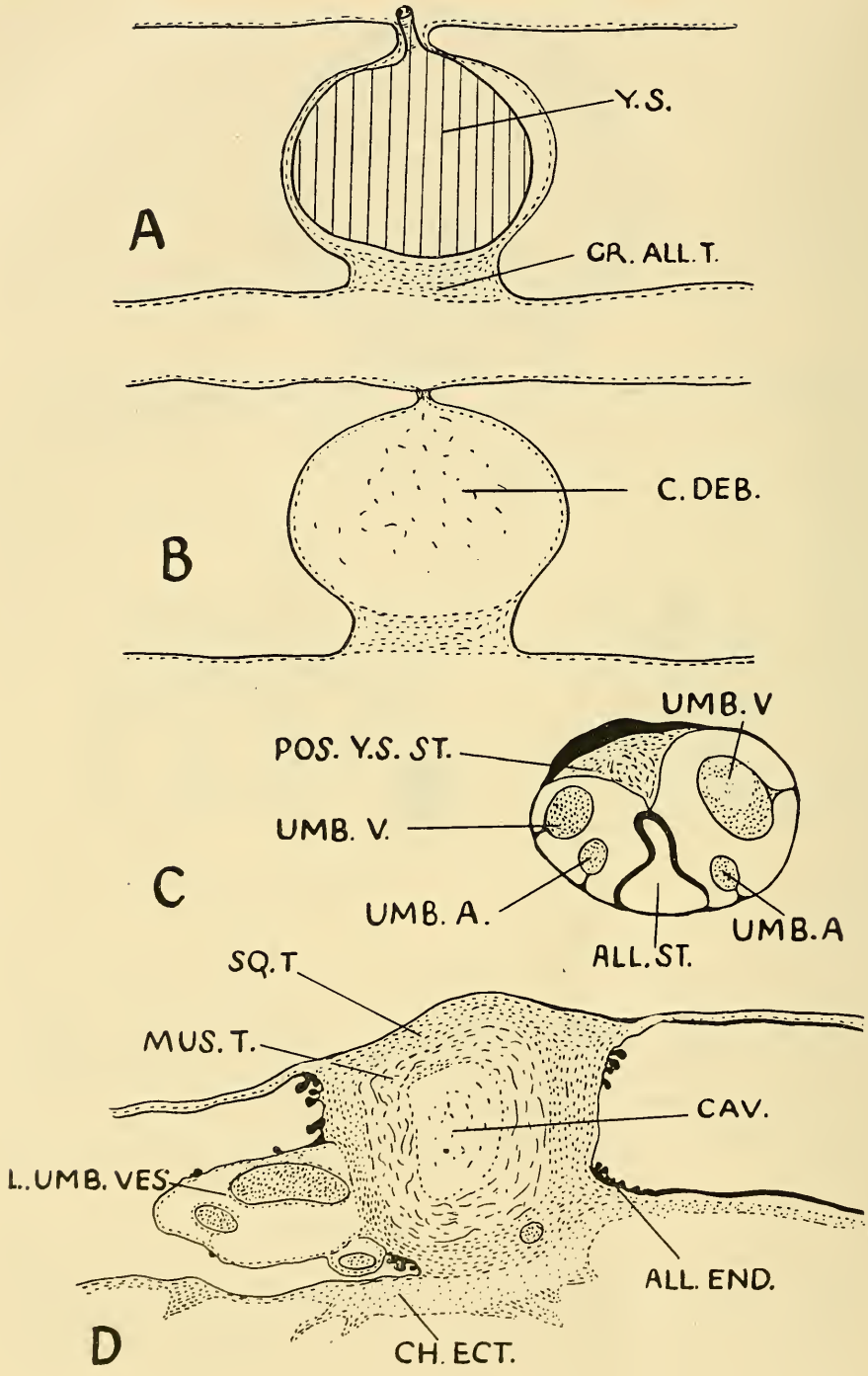
birth. Altogether four females were collected from Barrington Tops during the first two weeks of February, 1925, and the young are estimated to be about ten weeks old. Females were collected from the Blue Mountains during the last two weeks of January, 1927, and of these, five were kept until the 12th February, when the young were still unborn although those in the bush were born by the last week in January. By the 12th February all but two of the females had died, so it was thought advisable to open the remaining two and fix the contained embryos, which are taken as being at the stage immediately prior to birth, since it was obviously the captivity of the parents and not the condition of the young which inhibited birth. Three females were collected from Kiama during the first week of January, 1926, and were kept alive in Sydney until the end of the second week when the young were born.

The blastocyst taken from a female of the mountain type when the foetus is within one week of birth measures on an average 2 cm. in length and that from a coastal type 2·7 cm. When a female is opened up along the ventral body wall the yolk-sacs of the contained blastocysts are no longer conspicuous as in earlier stages, each being reduced to a small bag of yolk about 3 mm. in diameter, which may be in its normal position pressed against the overlying uterus, but is usually withdrawn from the latter until it lies hidden among the limbs and tail coils of the embryo. The embryo can be distinctly seen lying among its membranes, which are thin and greatly expanded by the large amount of embryonic excretion present in the allantoic vesicle. The excretion oozes out as a clear colourless fluid when the allantois is punctured. The embryos are well formed with definite scale markings and when touched wriggle about within their membranes. The limbs of some of the young lizards within a week of hatching were pressed against and almost embedded in the yolk-sac and in one instance the tail was coiled round it several times. This position of the limbs may indicate an effort on the part of the embryo to aid the withdrawal of the yolk-sac into its body, since some of the embryos when only about three weeks old were capable of movement when stimulated and even crawled for some distance when freed from their membranes.

From the sixth to the tenth week of the gestation period there is no marked decrease in the size of the yolk-sac, but during the eleventh and last weeks the reduction is pronounced, the sac decreasing to about one-twelfth its size at six weeks. The large cells described at Stage B as lining the upper surface of the yolk-sac now completely cover the sac, and by intense proliferation have filled the interior, which in section appears to be divided into numerous rounded areas usually composed of three or four cells surrounding a central blood vessel (Text-fig. 20, A and B). The cells are efficient yolk absorbers and rapidly empty the yolk-sac, passing the yolky material to the blood vessels. They are relatively enormous, each being definitely bounded and containing one large, deeply staining, irregular nucleus and many small or large vacuoles. The cell cytoplasm is stained a deep pink by eosin and is obviously packed with yolk material having the same appearance as the yolk granules. Many of the cells are actively ingesting yolk granules and their cytoplasm is packed with them, some completely filling the cell, others being extremely small and obviously prepared by the cells for their passage into the blood vessels (Text-fig. 20, C). The blood vessels encircled by the groups of cells are in many cases newly formed, haematopoiesis in the yolk-sac being active at this stage.



Text-fig. 20. A, section of yolk-sac of an eleven weeks old embryo showing the junction of the allantoic membranes at the base of the sac, the shell membrane and the "growth" of allantoic tissue; × 26. B, transverse section through the enlarged endoderm cells in the yolk-sac surrounding a blood vessel; × 562. C, section of a portion of the yolk-sac wall; × 562. D, section of the membrane formed by the junction of the outer allantoic membrane with the layers of somatic mesoderm, yolk-sac endoderm and chorionic ectoderm; × 562. ALL. MEMB., allantoic membrane; CH. ECT., chorion ectoderm; ENL. END. C., enlarged endoderm cell; F. GR. CH. ECT., finger-like growth of chorionic ectoderm; GR.T., growth of tissue; SH. MEMB., shell membrane; Y. GR., yolk-granules; Y.S., yolk-sac; Y.S. END., yolk-sac endoderm


A
Y.S.
CR. ALL. T.
B
C. DEB.
C
UMB. V
POS. Y.S. ST.
UMB. V.
UMB. A.
UMB. A
ALL. ST.
D
SQ. T
MUS. T.
CAV.
L. UMB. VES.
ALL. END.
CH. ECT.

With the reduction in size of the yolk-sac space is provided for the further extension of the allantois and at this stage the allantoic membranes completely envelop the yolk-sac, meeting and fusing at its base. The fusion is accompanied by a considerable growth of tissue (allantoic mesoderm and endoderm, Text-fig. 20, A; Pl. xl, fig. 6), which was observed in all the embryos examined and in the living condition was visible as a circular, flat, white area beneath the yolk-sac, or in the former position of the yolk-sac when the latter was no longer present. This "growth" of tissue varies in size, measuring on an average about half the diameter of the sac in the mountain type of blastocyst. The main mass of tissue is muscular with blood vessels embedded, and contains numerous yolk spheres and small dark granules which are possibly the remains of degenerating nuclei. Here, the vessels from the inner allantoic membrane pass to the outer allantoic membrane slung in thick folds of mesenchyme (Text-fig. 21, D) and lining the allantoic cavity the endoderm cells are similar in structure to those described above (Stage B, Text-fig. 16, A), having narrow bases and swollen apices. In this region they contain many small and a few large yolk-granules which, together with those in the main mass of tissue, were possibly derived from the outer layer of yolk-sac endoderm attached to the chorion and now overlying the outer allantoic membrane, these granules being passed intact from cell to cell. The under surface of the mass of proliferated tissue is bound by the chorionic ectoderm which formed part of the original foetal portion of the omphaloplacenta. The small yolk-sac now passes out from the encircling folds as indicated in Text-fig. 21, A and B, and into the gut of the embryo, where it is absorbed. The vitelline artery and vein with their branches are naturally withdrawn and absorbed with the sac. The yolk-sac stalk is torn away from the allantoic stalk and its position is marked by a thick proliferation of mesenchyme (Text-fig. 21, C).

The allantoic stalk contains a main artery and vein on either side as in earlier stages but the vessels are smaller. With the withdrawal of the yolk-sac and its stalk the allantoic stalk now appears to divide longitudinally a short distance from the body of the embryo, the upper stalk passing upwards and carrying an umbilical artery and vein which pass across the allantoic cavity as described at Stage B, the lower stalk passing downwards and carrying the remaining umbilical artery and vein directly to the allantoic membrane. In some embryos obtained from the Blue Mountains on 20th January, 1927, the yolk-sac was just entering the body and the ventral wall of the embryo was distended round the sac. After the removal of the sac the allantoic folds which surrounded it meet and join, a further proliferation of tissue occurring at the junction (Text-fig. 21, D), which is an extension of the original "growth" of tissue formed beneath the yolk-sac, and described above. There is a cavity at its centre containing corpuscles, debris and loose cells which were torn away from the yolk-sac when removed from the vicinity of the membranes and most of which are

Text-fig. 21. A, diagrammatic representation of the yolk-sac of an eleven weeks embryo encircled by the allantois. B, diagrammatic representation of the allantoic membranes immediately after the withdrawal of the sac. C, section of allantoic stalk showing the proliferated tissue in the former position of the yolk-sac stalk; × 30. D, section of the mass of proliferated allantoic tissue filling the former position of the yolk-sac; × 30. ALL. END., allantoic endoderm; ALL. ST., allantoic stalk; CAV., cavity; CH. ECT., chorion ectoderm; C. DEB., cell debris; GR. ALL. T., growth of allantoic tissue; L. UMB. VES., left umbilical vessels; MUS. T., muscular tissue; POS. Y.S. ST., position of yolk-sac stalk; SQ. T., squamose tissue; UMB. A., umbilical artery; UMB. V., umbilical vein; Y.S., yolk-sac.

now degenerating. The tissue is composed of a thick, inner muscular coat formed from the allantoic mesoderm, and a thick coat of uniform squamose cells formed from the allantoic endoderm, the outer layer of which consists of enlarged cells containing yolk granules. The amnion may be joined to the inner allantoic membrane and when so joined shares the fate of the allantois at the birth of the foetus. It is not known what becomes of the allantois at birth, since the young were born from the females in captivity while unobserved, but there were no membranes left in the uteri of these females, which were opened immediately upon the discovery of the birth of the young, which was approximately twenty-four hours later. It is possible that the young are born with these membranes attached as described for *T. scincoides* (Harrison, 1926), the embryos of which dispose of their membranes by biting the allantoic stalk and eating them. At birth the young lizards are quite able to fend for themselves, those born escaping out of the box and through several rooms into the open where they were found the day after birth.

The Omphaloplacenta.—As the yolk-sac is reduced in size the area of omphaloplacentation is naturally correspondingly reduced until, finally, when the yolk-sac is withdrawn from its position underlying the uterus and the allantoic membranes have extended under the sac, there is no longer an area of omphaloplacentation, since one of its main requisites, the foetal blood supply in the yolk-sac, is being removed with the sac, and its chorionic ectoderm is now part of the newly extended chorio-allantoic membrane. Allantoplacental modifications of maternal and foetal tissues extend under the yolk-sac in the place of the former omphaloplacental modifications, so that the maternal and foetal tissues in this region are twice modified for placentation. However the position of the omphaloplacenta is marked until the time of birth by the remains of enlarged chorionic ectoderm cells which line the mass of proliferated tissue at the junction of the allantoic membranes beneath the yolk-sac (Text-fig. 21, D).

The Allantoplacenta.—As the allantois grows under the yolk-sac the outer allantoic membrane unites with the layers of somatic mesoderm and chorionic ectoderm so that a peculiar arrangement results, where instead of the normal chorio-allantoic membrane forming the foetal portion of the allantoplacenta, a membrane is established which contains in addition a layer of yolk-sac endoderm between the chorionic ectoderm and the outer allantoic membrane (Text-fig. 20, D). The condition of the foetal tissues of the allantoplacenta is further complicated by the previous modification of the chorionic ectoderm for its functioning as part of the omphaloplacenta. However it is remodified for allantoplacentation by its degeneration over the surface of the placental face, with the exception of the area underlying the mass of tissue formed at the junction of the allantoic membranes. Here the chorionic ectoderm is composed of many cell layers, the cells resembling those of the omphaloplacental region described at Stage B, being enlarged and irregularly shaped, with the lower layers squamose. The "finger-like" down-growths of cells are present among the folds of the shell membrane and are sometimes disconnected from the rest of the chorionic ectoderm and lie loose among the folds. Over the rest of the newly extended allantoplacental area with its well vascularized outer allantoic membrane, the chorionic ectoderm partly degenerates (Text-fig. 22, B), and is only represented by the isolated enlarged cells which serve to attach the foetal tissue to the uterus and which are characteristic of the main allantoplacental area. The layer of yolk-sac endoderm beneath the chorionic ectoderm also degenerates, the contained yolk granules being

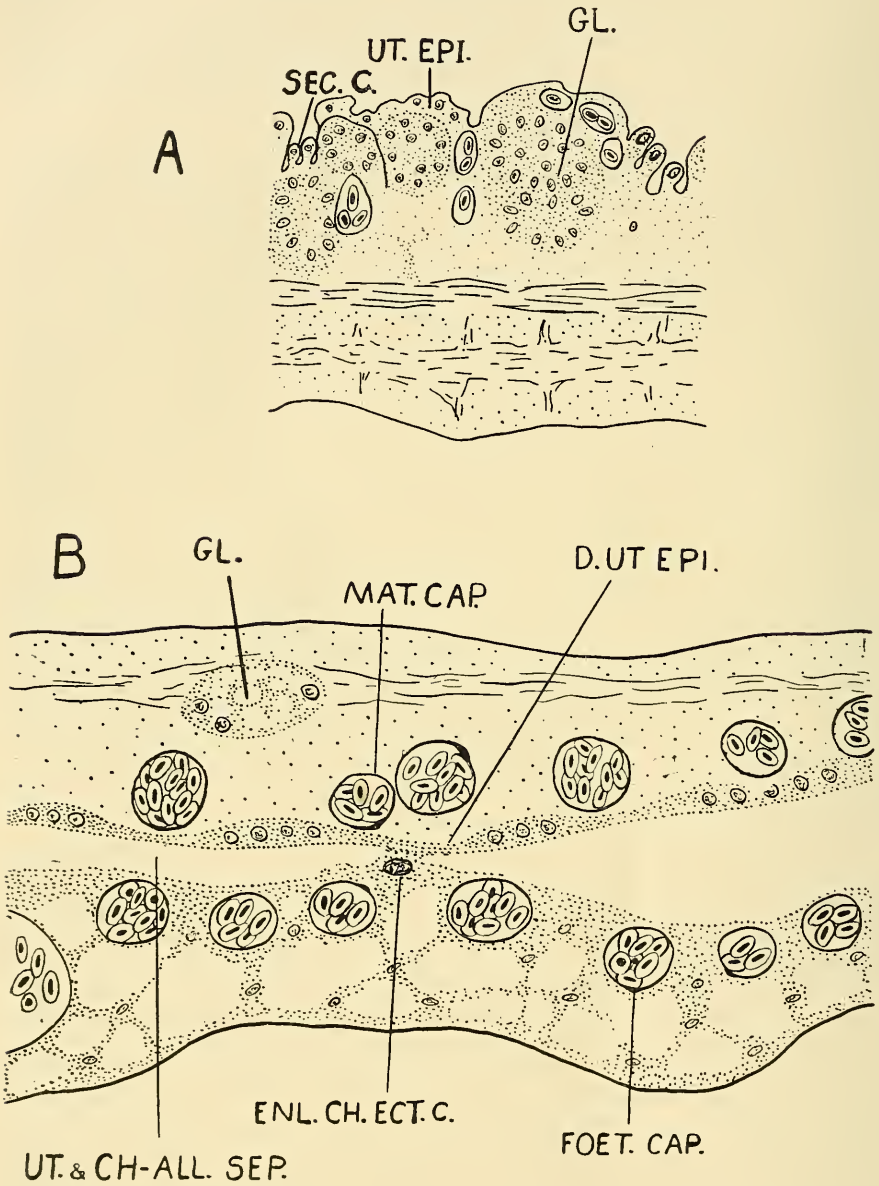
absorbed by the underlying allantoic tissue. The degeneration of the chorionic ectoderm and yolk-sac endoderm is probably directly due to the presence of the underlying allantoic capillaries, since, in the region of the junction of the allantoic membranes where the thick pad of tissue underlies the chorionic ectoderm and yolk-sac endoderm instead of numerous allantoic capillaries, the chorionic ectoderm and yolk-sac endoderm remain practically intact.

The changes which occur in the allantoic membrane in this region correspond to those which occur in the main allantoplacental region, the capillaries invading the overlying degenerating foetal tissue. The numerous capillaries are typically round, packed with corpuscles and have thin walls, and before the degeneration of the chorionic ectoderm and yolk-sac endoderm lie embedded in a thick coat of mesenchyme (Text-fig. 20, D), but after the degeneration of these tissues they may take up the whole width of the allantois. The pad of shell membrane is in the same position and in much the same condition as in earlier stages, having the same coagulum among its folds. The fate of the shell membrane at the birth of the foetus is not known, it being either absorbed before birth by the foetal tissues, removed with the foetus at birth or left behind in the uterus and subsequently absorbed. It is unlikely that the foetal tissues can absorb such a quantity of membrane in the few remaining days before birth, since it remained practically intact at the base of the yolk-sac for two months.

The extension of the allantois and the modification of the foetal tissue is accompanied by a change in the structure of the overlying uterine wall, the maternal tissue being modified for some distance beyond its proximity to the allantois, as at Stage A. The uterus passes from a condition of modification for omphaloplacentation, where it is thick, with small capillaries overlying a layer of fairly deep columnar epithelium, to a condition of modification for allantoplacentation, where the epithelium degenerates and the capillaries enlarge and pass to the surface of the uterus (Text-fig. 22, B). Over some areas the epithelium may remain intact but in a reduced condition as a layer of small cells, however, there are large areas where the degeneration is as marked as in the main allantoplacental region.

Where the uterus was previously slightly folded in the omphaloplacental region, an interesting condition results when the tissues are remodified for allantoplacentation (Text-fig. 22, A). Each fold is mainly filled by vacuolated glandular tissue, containing many small round nuclei. Between the folds there may be large oval capillaries while numerous smaller, typically rounded capillaries lie at the surface of the folds either exposed or covered by a thin layer of epithelium. In the crevices between the folds where the maternal capillaries are comparatively widely separated from the foetal capillaries the epithelial cells do not degenerate but become enlarged and glandular, with narrow bases and swollen apices (Text-fig. 22, A), and function for food secretion. Early in this investigation only advanced stages in the development of the placenta were available and upon the discovery of such an area of placentation it was at first thought to represent the type of allantoplacentation for *L. quoyi*. However the study of earlier stages has clearly shown that this area was originally modified for omphaloplacentation and its present folded structure is a result of such modification.

The females kept in cavity until the 12th February contained embryos which are taken to be at a stage immediately prior to birth, where the yolk-sac is completely withdrawn into the body of the embryo and the allantoic membranes from both sides of the yolk-sac have met and fused. In the main allantoplacental



Text-fig. 22. A, section of the folded uterine wall remodified for allantoplacentation; × 460. B, section of the allantoplacental region in the former position of the omphaloplacental region; × 613. D. UT. EPI., degenerating uterine epithelium; ENL. CH. ECT. C., enlarged chorionic ectoderm cell; FOET. CAP., foetal capillary; GL., gland; MAT. CAP., maternal capillary; SEC. C., secretory cells; UT. EPI., uterine epithelium; UT. & CH. ALL. SEP., uterus and chorio-allantoic membrane separated.

region of these embryos the maternal and foetal tissues are much thinner, the muscle layers and glands of the uterus being markedly flattened. The maternal and foetal capillaries are not as numerous nor as full of corpuscles as in earlier stages and the foetal tissue is easily separated from the maternal wall when dissecting or sectioning the material.

It is thought that the structure of the uterus changes in anticipation of allantoplacentation and not as a result of stimulus from the immediate proximity of the allantois, since it will be recalled that in embryos examined one week after fertilization, the uterus shows early indications of placental modification when the allantois is merely a small swelling at the posterior end of the embryo; also the uterus overlying the edge of the yolk-sac is modified for placentation before the extension of the allantois to its vicinity; in addition, in some embryos eleven weeks old the allantois underlying the yolk-sac is covered by a thick coat of chorionic ectoderm cells and the conditions resemble those of omphaloplacentation, the uterine wall being in contact with and having its materials absorbed by the specialized chorionic ectoderm, yet here the uterus does not retain its omphaloplacental modifications, but is well modified for allantoplacentation; also the uterus is modified for allantoplacentation even when separated from the allantois by a thick pad of shell membrane. However it may be regarded as peculiar that the modification progresses roughly parallel with the extension of the allantois and does not occur simultaneously over the uterus, and this may be taken as indicating a direct relationship between the two processes, but it is most probably a result of the uterus retaining its omphaloplacental modifications and only replacing them by allantoplacental modifications as the foetal omphaloplacentation yields to allantoplacentation.

The modification of the foetal and maternal tissues for allantoplacentation as late as the last two weeks of the gestation period shows that the allantoplacenta is essential until the birth of the foetus.

4. *Period after birth.*

Females were available in a condition ranging from one day to one week after the birth of the young. In these females the uteri were thick, much convoluted and distinctly restricted into incubatory chambers. The wall of the uterus extracted from one of the females one day after the birth of the young measures about 0·4 mm. in its thickest part, the muscle layers being thicker than in the normal non-pregnant condition and the glands having partly regained their normal shape and structure. The cytoplasm of the gland cells encloses small yolk granules derived from the debris in the cavity of the uterus, and the granules are also present in the epithelial cytoplasm. The inner surface of the uterus is thrown into deep folds which are covered by a thin layer of regenerating epithelium. However the capillaries are still concentrated at the surface of the mucosa and in places are almost exposed and have the typical rounded appearance of the capillaries in the allantoplacental region. The epithelial cells are largest in the crevices between the folds, being narrow and columnar with an oval nucleus at the base. The uterine cavity contains a dark staining coagulum mixed with yolk spheres and cell debris which fills the crevices between the folds and is being rapidly absorbed by the uterus.

At the end of the first week after the birth of the young the uterus is more normal in structure, but is still obviously influenced by the preceding gestation period. Its wall is thinner but the glands have not completely regained their

normal structure, the nuclei being still grouped closely together. The mucosa contains many more small capillaries than in the normal condition, but the epithelial cells, although as yet comparatively small, are uniformly arranged over the surface of the uterus, the majority being definite and columnar. Most of the coagulum in the cavity has been absorbed and there are fewer yolk spheres in the mucosa.

IV. Comparison with the Lizards *Chalcides tridactylus*, *Lygosoma* (*Liolepisma*) *entrecasteauxi* and *Tiliqua scincoides* and with the Marsupial *Perameles*.

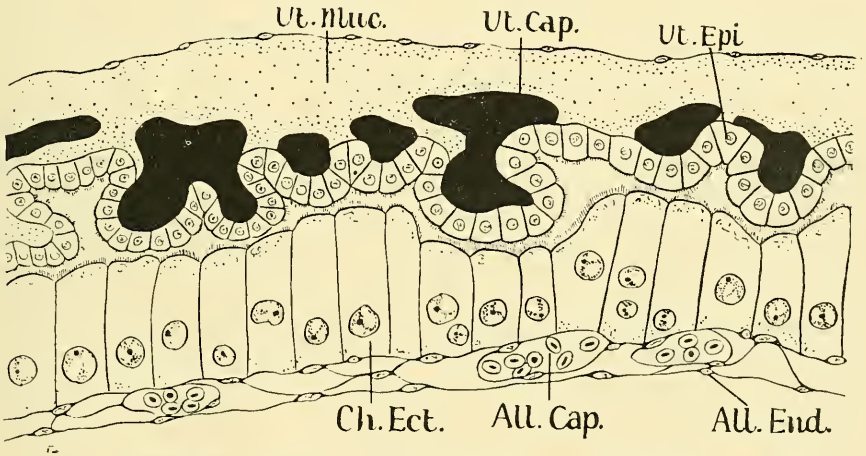
(*a*). Comparison with *C. tridactylus* and *L. entrecasteauxi*.

The structure of the allantoplacenta in *L. entrecasteauxi* is so remarkably similar to that in *C. tridactylus* that it is unnecessary to compare and contrast the placenta in each with that in *L. quoyi*. *L. entrecasteauxi* has been chosen in preference to *C. tridactylus* for a detailed comparison with *L. quoyi*, since the author has described the placentation of that lizard in conjunction with Professor Harrison (Harrison and Weekes, 1925), and since material is available for examination in the sectioned and unsectioned condition.

The discovery of allantoplacentation in *L. entrecasteauxi* and in *L. quoyi*, two species of the one genus *Lygosoma*, is more important than might be at first supposed, since their methods of allantoplacentation differ more than might be expected after a study of the placenta in related species of mammals. The two lizards were collected from Barrington Tops and Mount Kosciusko, although *L. quoyi* was restricted to the marshy regions and *L. entrecasteauxi* to the hills surrounding them. *L. entrecasteauxi* is a much smaller lizard than *L. quoyi*, being about one-third the size of the coastal type of the latter, and its eggs are correspondingly smaller. However, although the yolk-sac is only about one-third the size of that in *L. quoyi* the omphaloplacenta is more highly developed. In the stages available for examination there was no indication of the abnormal growth of the extra-embryonic mesoderm into yolk-sac, but this may be evident in earlier stages. The omphaloplacenta of *L. entrecasteauxi* differs from that in *L. quoyi* in that the cells of the uterine epithelium are much larger and more uniform in structure; the chorionic ectoderm cells are also larger, there being a single row of evenly enlarged cells with large dark nuclei, in the place of the multilayered chorionic ectoderm in *L. quoyi* with its cells varying in length and shape; the area of omphaloplacentation is relatively greater and this is thought to be due to the absence of the thick pad of shell membrane in the embryos of *L. entrecasteauxi* examined and its invariable presence in the omphaloplacental region of *L. quoyi*.

Harrison and Weekes (1925, p. 475) describe the maternal portion of the allantoplacenta as being restricted to "a fusiform to elliptical opaque whitish area" and the extent of the foetal placentation as slightly exceeding that of the maternal placental area. In *L. quoyi*, however, the placental area is not restricted, modifications of maternal and foetal tissue occurring over the entire area embraced by the allantois. In *L. entrecasteauxi* the elliptical placental area is marked by complicated villous folds of the maternal wall which can be seen with the unaided eye, but in *L. quoyi* the placental face is smooth and discernible only in sectioned material. As well as the differences in general appearance, the histological differences between the two allantoplacentae are marked. In the placenta of *L. entrecasteauxi* two elliptical epithelial sheets with every cell clearly bounded are closely apposed but are in no way joined or fused (Text-

fig. 23). The epithelium lining the maternal ridges is composed of enlarged ciliated cells. The villous folds impress their form upon the closely underlying ciliated chorionic ectoderm causing irregularities in its surface and variations in the size of the cells, some growing up into the crypts and being extremely elongated, in all cases being twice as long as they are wide. The maternal folds are fed by large capillaries while the foetal vascular network lies close at the base of the chorionic cells and is bound internally by a sheet of mesenchymatous connective tissue of varying thickness. In *L. quoyi* the maternal wall is not covered by enlarged ciliated epithelial cells, there being at the most a thin bounding layer of epithelial protoplasm with occasional nuclei embedded; there is a network of small rounded maternal capillaries instead of the few large capillaries in the villous folds of *L. entrecasteauxi*, and these are exposed at the surface of the uterus and do not lie beneath a thick epithelial layer; the foetal tissue is attached to the maternal wall, the attachment being efficient although superficial; the cells of the chorionic ectoderm do not become enlarged but degenerate, allowing the allantoic capillaries to bulge at the surface, so that the maternal and foetal blood streams are in close apposition.



Text-fig. 23. Section of the elliptical allantoplacental area in *L. entrecasteauxi*. All. Cap., allantoic capillary; All. End., allantoic endoderm; Ch. Ect., chorionic ectoderm; Ut. Cap., uterine capillary; Ut. Epi., uterine epithelium; Ut. Muc., uterine mucosa.

Hence it can be seen that the allantoplacenta in *L. quoyi* is fundamentally different from the elliptical and restricted allantoplacental region in *L. entrecasteauxi*, since food transition in *L. quoyi* is carried on by the apposed maternal and foetal bloodstreams and not by the glandular activity of the uterine epithelium and the phagocytic and absorbing powers of the chorionic ectoderm as in *L. entrecasteauxi*.

The omphaloplacenta in *C. tridactylus* (Giacomini, 1891, p. 348) "se forme tardivement et reste rudimentaire" consisting of enlarged chorionic ectoderm cells in the region of the yolk-sac. No mention is made of any modification of the uterine tissues in this region. It is possible that the development of the omphaloplacenta

may be restricted by the small size of the eggs (2·5 to 3 mm.) in such a comparatively large lizard. The growth of the extra-embryonic mesoderm into the yolk-sac in *L. quoyi* has no parallel in *C. tridactylus* since Giacomini says, 1891, p. 343, "tant que les oeufs ne sont pas arrivés à un certain degré de développement, la connexion immédiate entre l'ectoblaste et l'entoblaste vitellin persiste telle qu'elle a été décrite. Le feuillet moyen s'arrête aux limites de la connexion, de sorte que, pendant quelque temps, la paroi vitelline, sur ce point, est privée de sa structure caractéristique, et ne se trouve pas vascularisée. Dans des états avancés de développement, le mésoderme envahit aussi la région en question, laquelle, alors, est également vascularisée". This is the only reference Giacomini makes to the growth of the extra-embryonic mesoderm over the yolk-sac and it is taken to mean that the sinus terminalis remains quiescent for some time at the outer limits of the area of junction of the chorionic ectoderm with the yolk-sac endoderm, finally continuing its growth round the sac in the normal way between the ectoderm and endoderm.

An interesting and important phenomenon has been observed in the placentation of *L. entrecasteauxi* since the publication of the papers by Harrison and Weekes, 1925, and Weekes, 1927. The area of apposed maternal and foetal tissue in *L. entrecasteauxi* other than the omphaloplacental and the elliptical allantoplacental areas was regarded as unimportant and non-placental in the investigation in 1925, the maternal and foetal tissues being so thin and flattened here that it was difficult to make a histological study of them. However in one of the series of sections a relatively thick area was recently observed, attention being first arrested by the very close attachment of the foetal to the maternal tissues in this region which persisted even when the tissues in the elliptical allantoplacental area were fairly widely separated. Upon a closer examination it was found that the structure of this region corresponds closely to that of the allantoplacenta in *L. quoyi*. The maternal and foetal epithelial cells have degenerated, the epithelial nuclei in the maternal wall are grouped between the capillaries and have the same typical rounded appearance as in *L. quoyi*, and the foetal tissue is attached to the maternal tissue by scattered enlarged chorionic ectoderm cells. The only obvious differences between the structure of this region and that of the allantoplacenta in *L. quoyi* are the smaller number of maternal and foetal capillaries, their ellipsoid cross section and the presence of a thick coat of mesenchyme underlying the foetal capillaries. It is thought that in younger stages in the development of *L. entrecasteauxi* this specialized region may be more extensive.

It will be recalled that at Stage B a condition of allantoplacentation is described for one of the embryos of *L. quoyi* examined, where the uterine wall and chorio-allantoic membrane are thrown into rudimentary folds and where the epithelium of the maternal folds has not degenerated, and where, in addition, the chorionic ectoderm cells have not degenerated to the same extent as in the allantoplacenta of other embryos, a few of them being larger than in any of the other allantoplacentae examined. When this folded area is compared with the elliptical placental area of *L. entrecasteauxi* the resemblances are noticeable. The position of the folds in the region of the main longitudinal artery and vein resembles the position of the folds in *L. entrecasteauxi*; the maternal epithelial tissue obviously plays the important part in food secretion since the capillaries are not present at the surface of the uterus, and since the epithelial cells are enlarged and obviously modified for secretion; the chorionic ectoderm cells are comparatively large and contain enormous nuclei, the shape of the cells being to

some extent modified by the shape of the overlying uterine wall; and finally, the foetal capillaries lie at the bases of the chorionic ectoderm cells.

There are, however, many differences. The area in *L. quoyi*, although in a much larger lizard, is only half the width of that in *L. entrecasteauxi* and the folds are only rudimentary when compared with the well formed complicated folds in that lizard; the uterine epithelial cells vary in shape and size and are not ciliated nor uniformly enlarged nor arranged; the chorionic ectoderm cells are neither ciliated nor granular and are not definite in shape, cell boundaries being recognizable only at the free margins and in addition in some places they are degenerating and the allantoic capillaries passing to the surface; there is no deep layer of mesenchymatous tissue underlying the chorion and the allantoic capillaries.

The significance of the occurrence of the second type of allantoplacentation in *L. entrecasteauxi* and of the folded area in one of the embryos of *L. quoyi* examined will be discussed below.

(*b*). Comparison with *Tiliqua scincoides*.

T. scincoides is a much larger lizard than either *L. entrecasteauxi* or *L. quoyi* and is slightly larger than *C. tridactylus*. The habitat of this lizard resembles that of *L. quoyi* in that it varies from sea level to an altitude of 3,000 feet. The pregnant females contain a greater number of young than those of *L. quoyi*, the two described by Flynn (1923) containing eleven and fifteen. The general disposition of the blastocyst is the same as in *L. quoyi*.

According to Flynn the yolk-sac circulation of *T. scincoides* extends over the outer surface of the sac with the exception of a small area at the lower pole. In *L. quoyi* the circulation completely surrounds the sac. Flynn notes (1923, p. 75) that "a sinus terminalis could not be definitely made out". This was since discovered (Weekes, 1927) to be due to the downgrowth of the extra-embryonic mesoderm into the yolk-sac as in *L. quoyi*. The omphaloplacenta in *T. scincoides* (Weekes, 1927) is much more highly specialized than that of *L. quoyi*, the uterine wall being thrown into definite villous folds which are visible to the unaided eye, and the cells of the epithelium are much larger and more regular than those of the maternal epithelium in *L. quoyi*. It is possible that the rudimentary folding of the uterine wall in *L. quoyi* is the forerunner of such a specialized condition. The most outstanding differences between the omphaloplacentae are the regular folding of the foetal tissue in *T. scincoides* to fit into the maternal crypts and the regular modification of the chorionic ectoderm cells.

The omphaloplacenta in both lizards is of the same type. the food transition being carried on by apposed maternal and foetal epithelial faces, and the foetal tissues vascularized by vessels embedded in the yolk-sac and separated from it by the extra-embryonic coelome.

The general relationship between the allantois and the embryo is the same in both lizards with one exception. In *Tiliqua* (Flynn, 1923, p. 77) the allantoic stalk passes downwards and outwards while in *L. quoyi* it passes upwards and outwards. The method of transference of blood vessels across the allantoic cavity in the two lizards has been compared at Stage B. In both lizards the inner allantoic membrane fuses with the amnion, but as Flynn does not mention any connection between the chorio-allantoic and the inner allantoic membranes. it seems that as far as those lizards for which placentation has been described are concerned, this arrangement is peculiar to *L. quoyi*. The area of allantoplacenta-

tion in *T. scincoides* is smaller than that in *L. quoyi* since its extension is restricted by the central portion of the allantois alone becoming attached to the chorion, the marginal zone being free and unattached. Flynn gives no figures illustrating the histological relations in the allantoplacenta of *Tiliqua* and it is therefore difficult to compare the placenta with that in *L. quoyi*. He says (1923, p. 76) that "the union between chorion and uterine epithelium is very intimate. The uterine epithelium apparently consists of a single layer of very flattened cells, while the chorionic ectoderm has proliferated greatly, is much vacuolated, resembling a typical plasmodium and is formed in the main of markedly enlarged cells with large nuclei and connected together by amoeboid processes. These processes insinuate themselves into and between the maternal cells in much the same way as Hill has described for the chorionic cells in the formation of the metrioplacenta of *Dasyurus viverrinus*". No special mention is made of the maternal circulation and in describing the foetal circulation Flynn says (1923, p. 77) that the allantoic vessels "ramify through the mesenchymal layer of the placental face", but makes no mention of any unusual position of the allantoic capillaries. It is evident from these observations and the above description of the placental area that there is not the same degeneration of epithelial surfaces and apposition of capillaries as in *L. quoyi*. The "very flattened cells" of the uterine epithelium may present a stage intermediate between the condition of enlarged cells in *C. tridactylus* and *L. entrecasteauxi* and of degenerated epithelium in *L. quoyi*. Hence it is deduced that the maternal and foetal epithelial tissues in *Tiliqua*, although not enlarged to the same extent as in *C. tridactylus* or *L. entrecasteauxi*, carry on the function of food transition and therefore the type of placentation differs essentially from that in *L. quoyi*. However, the two types have in common the attachment of the foetal tissues to the maternal wall, both being of the conjoint type, and the establishment of this attachment by enlarged chorionic ectoderm cells which do not invade the maternal tissue to any extent, the attachment in each being superficial.

(*c*). Comparison with *Perameles*.

Perameles is the only marsupial for which allantoplacentation has been recorded. The placentation of *Perameles* was described by Hill (1897), redescribed by Flynn (1923), and these authors hold different opinions as to the nature of the placenta. Hill claims (1897, p. 387) that the uterine mucosa undergoes hypertrophy; that the vessels in the mucosa increase in size and number; that the uterine epithelium changes into a vascular syncytium, the nuclei becoming grouped together in nests situated in lobular projections of the deeper surface of the syncytium; and that the maternal capillaries pass up between the syncytial lobules and form a network beneath the epithelial protoplasm. He claims further that the embryo becomes attached to the prepared maternal wall by means of enlarged chorionic ectoderm cells, which eventually degenerate over the placental area proper; that the allantoic capillaries now directly reach the vascular surface of the maternal placental syncytium to which they become intimately attached, dipping down into the depressions on its surface and forming a regular interlocking system, and that finally the foetal and maternal blood streams are now only separated by their thin endothelial walls and perhaps a layer of syncytial protoplasm.

Flynn claims that the chorionic ectoderm does not completely degenerate but actively invades the maternal tissues and thus brings the type of placentation

found in *Perameles* in line with that found among the eutherian mammals, more especially the Carnivora "where there are the same characteristics of passivity of uterine epithelium and activity of the trophoblast".

By the kind permission of Professor Harrison of the Zoology Department, University of Sydney, I have been able to obtain some of the *Perameles* material prepared by Hill and used by him and Flynn. This consists of two slides, one containing sections of the placenta of an embryo 7 mm. in direct length and the other of one 1·5 mm. in length. An examination of this material has convinced me that Flynn's interpretation of the structure of the placenta is the correct one. The most important and convincing evidence is the invasion of the deep maternal syncytial lobules by the large nuclei of the trophoblast, which is so plainly evident that as Flynn himself says it is impossible that there can be any other conception than the one he suggests. Flynn has ably and thoroughly discussed the placenta in *Perameles* (1923), and there is no need for further comment here, but while I agree with his interpretation of the structure of the placenta I do not support his claim that its similarity to that of the placenta in some of the Carnivora is of fundamental phylogenetic importance.

The relationship between the embryo, its yolk-sac and the allantois in *L. quoyi* is somewhat similar to that in *Perameles*, allowance being made for the difference in the relative size of the yolk-sac and the allantois in each, the yolk-sac in *Perameles* occupying the main portion of the blastocyst and the allantois being restricted to the remaining portion. In each the embryo is sunk down into the yolk-sac being partially surrounded by the yolk-sac wall and the yolk-sac is vascularized by one main artery and vein. But the vascularization does not completely cover the sac in *Perameles* as in *L. quoyi*, there being a definite sinus terminalis present, and the method of the growth of the extra-embryonic mesoderm over the sac is normal. The vascularization of the allantois is similar in both, each of the two main arteries being accompanied by one of the veins in its ramifications over the placental face, the arrangement being confined to the main trunks. However there are none of the "cellular bridges" passing across the allantoic cavity in *Perameles* as in *L. quoyi*, possibly on account of the smallness of the allantoic vesicle and the consequent lack of any need for a short cut for the vessels. In both, the allantoic stalk enters the body of the embryo immediately posterior to the yolk-sac stalk, but in *L. quoyi* both stalks are joined by mesenchyme and have the appearance of one.

There is little similarity between the omphaloplacentation of these forms, since in *Perameles* the uterine epithelium degenerates to form a syncytium with the maternal capillaries at the surface, the capillaries being closely apposed to a flat layer of chorionic ectoderm which is separated by blood vessels from a layer of enlarged yolk-sac endoderm cells.

According to Flynn's interpretation of its structure, the allantoplacenta in *Perameles* consists of a fused area of complexly folded maternal and foetal tissue. The maternal wall is thick and modified for the attachment of the foetal tissue by the proliferation of the nuclei of the epithelium and their migration to the deeper parts of the epithelium which has now markedly thickened, the result being the formation of a syncytium in which the deeply situated nuclei assume a particular form and arrangement. Flynn (1923, p. 137) says "the nuclei become aggregated mainly in rounded masses or nests situated in the lobular projections of the syncytial protoplasm. The lower surface of the syncytium has a wavy appearance due to the presence of the lobules . . . at this stage the syncytium

is well vascularized, each capillary being enclosed in its delicate endothelial layer". The maternal capillaries pass up between the lobules and form a network at the surface of the epithelial protoplasm. To this prepared maternal tissue the chorion attaches itself by a single layer of enlarged ectoderm cells. These cells divide (p. 141) "to give rise to nucleated groups in which cell outlines have disappeared. . . . At various points these nuclei invade the uterine syncytium and the remaining basal cells of the trophoblast layer form the cytoblast or cytotrophoblast". Further (p. 167) "the outward migration of the basal cytoblast cells where converted into plasmodiblast gives opportunity for the maternal and foetal vessels to come into intimate apposition . . . all maternal vessels have definite endothelial walls, hypertrophy of the endothelial cells does not occur and lacunae are not formed". In my own observations most of the maternal capillaries were seen to lie immediately above the allantoic capillaries, both sets of capillaries being round.

The following are the main differences between the placentation of *Perameles* and that of *L. quoyi*.

1. The uterus in *Perameles* is much thicker than that in *L. quoyi*, and the uterine epithelium is deeper both before and after it is modified for placentation, and when modified is constricted into lobules containing distinct nests of nuclei, which arise by proliferation.

2. There is no shell membrane and the foetal tissue is attached to the maternal wall before the fusion of the allantois with the chorion.

3. The enlarged chorionic ectoderm cells proliferate and invade the maternal syncytium, firmly fixing the foetal tissue in position and absorbing food by their phagocytic action.

However the points in common are outstanding and fundamental.

1. The uterine epithelium in *L. quoyi*, although a narrow layer degenerates and forms a syncytium containing the rounded, palely staining nuclei which resemble those of the syncytial lobules in *Perameles* in structure and in that they "lack staining qualities" (Flynn, p. 137).

2. The maternal capillaries multiply and invade the degenerating epithelial cytoplasm and pass to the surface of the uterus.

3. The foetal tissue is attached to the maternal wall by enlarged chorionic ectoderm cells which remain throughout the life of the placenta.

4. The maternal and foetal capillaries are closely apposed, being separated only by their thin endothelial walls and perhaps a layer of maternal and foetal cytoplasm. The capillaries have definite endothelial walls, hypertrophy of the cells does not occur and the foetal capillaries lie beneath the maternal.

Some of the differences, however, are due to the natural conditions in *L. quoyi*. The narrowness of the uterine epithelial layer does not lend itself to the formation of a deep syncytium, and the presence of the shell membrane hinders the early fixation of the chorion to the uterine wall. So that, the only important difference between the placentae is, that in *Perameles* the chorionic ectoderm proliferates and invades the maternal syncytium, whereas in *L. quoyi*, with the exception of scattered enlarged cells, it degenerates. Hence can be seen the similarity between the two types of placentation and the reason for the statement in the previous paper on the placentation of *L. quoyi* (Weekes, 1927, p. 29) that the allantoplacenta in *L. quoyi* more closely resembles that of the Mammalia than any hitherto recorded in a reptile.

V. Theoretical Considerations.

A discussion of the relationship of the placentation of *L. quoyi* with that of other reptiles, and of its similarity to the placentation of the marsupial, *Perameles*,

must be deferred until an examination of other viviparous forms of reptiles is made. Also the as yet undescribed placentation of *E. whitei* and *E. striolata*, which closely resembles that of *L. quoyi*, must be taken into consideration. However, attention is called to a statement (Weekes, 1927, p. 29) that "in the genus *Lygosoma* two members, namely *L. entrecasteauxi* and *L. quoyi* have each developed distinct types of placentation". This is true for the folded elliptical area of placentation in *L. entrecasteauxi*, but with the discovery of the second area of placentation (described above) the difference between the two types is no longer so marked. It may be that the placentation in these two lizards is related, the common ancestral type being similar to that in *L. quoyi*, the placentation of *L. entrecasteauxi* becoming independently specialized by the development of the restricted elliptical region; or it may be that placentation was independently acquired by each, by *L. entrecasteauxi* before *L. quoyi*, this supposition being supported by the absence of shell membrane in *L. entrecasteauxi* and by its presence and the rudimentary condition of the omphaloplacenta in *L. quoyi*. The folded area in one of the embryos of *L. quoyi* examined might be regarded as representing a developing area in *L. quoyi* such as occurs in *L. entrecasteauxi*, but it is probably only a freak in placental development, since it occurs in only one of the many embryos examined.

VI. *Summary and Conclusions.*

The placentation of the Scincid lizard *Lygosoma* (*Hinulia*) *quoyi* is described in detail in the present communication and compared and contrasted with that in the Scincid lizards *Chalcides tridactylus*, *Lygosoma* (*Liolepisma*) *entrecasteauxi* and *Tiliqua scincoides* and with that in the marsupial *Perameles*. The following is a summary of the work and of the main conclusions drawn.

1. The lizard is not strictly viviparous, there being a shell membrane present which accumulates at the base of the yolk-sac as a thick pad in advanced stages of development.
2. An omphaloplacenta is present which even in its mature condition is less specialized than that in *L. entrecasteauxi*, *T. scincoides*, *E. whitei* and *E. striolata*.
3. An allantoplacenta of the conjoint type is present consisting of degenerated maternal and foetal epithelial tissue and apposed maternal and foetal blood streams.
4. A modification of the structure of the allantoplacenta occurs in some embryos by the junction of the inner allantoic membrane and the amnion with the placental area.
5. The right umbilical artery and vein pass to the allantoplacental region across the allantoic cavity and the method of the establishment of its passage is described.
6. The placentation of *L. quoyi* is described as being different from that in *L. entrecasteauxi* and *C. tridactylus*, where the function of food transition is mainly carried on by the modified maternal and foetal epithelial tissues.
7. The occurrence of a second area of allantoplacentation in *L. entrecasteauxi* is recorded, the structure of which resembles that of the allantoplacentation in *L. quoyi*. No deductions are made at this stage, a further study of possible placentae among the other viviparous members of the genus *Lygosoma* being necessary.
8. After an examination of some of the *Perameles* material used by both Hill and Flynn, Flynn's interpretation of the structure of the allantoplacenta in *Perameles* is supported in this communication.
9. The type of allantoplacentation in *L. quoyi* is found to be essentially similar to that in the marsupial *Perameles*, with differences in detail.

References.

CALDWELL, 1895.—On the Arrangement of the Embryonic Membranes in the Marsupial Animals. *Quart. Journ. Micr. Sci.*, xxxvi.

DUVAL, 1892.—Le Placenta des Rongeurs. *Journ. de l'Anat. et de la Phys.*

FLYNN, 1922.—The Phylogenetic Significance of the Marsupial Allantoplacenta. PROC. LINN. SOC. N.S.W., xlvii, 4.

FLYNN, 1923.—The Yolk-sac and Allantoic Placenta in *Perameles*. *Quart. Journ. Micr. Sci.*, lxvii, 1.

————, 1923.—On the Occurrence of a true Allantoplacenta of the conjoint type in an Australian Lizard. *Rec. Aust. Mus.*, xiv.

GIACOMINI, 1891.—Matériaux pour L'étude du développement du *Seps chalcides*. *Arch. Ital. de Biol.*, xvi. (Reprint from *Monitore Zool. Ital.*, ii, Nos. 9-10.)

————, 1891A.—Über die Entwickelung von *Seps chalcides*. *Anat. Anz.*, vi.

————, 1893.—Contribution à la connaissance des annexes foetales chez les reptiles, 1er et 2e. Note préventive. *Arch. Ital. de Biol.*, xviii. (Abstract of paper in *Monitore Zool. Ital.*, iv, No. 7, 1893.)

————, 1893.—Sur l'oviducte des Sauropsides. *Arch. Ital. de Biol.*, xxi, 1894. (Abstract of paper in *Monitore Zool. Ital.*, iv, Nos. 10-12.)

————, 1893.—Nouvelle contribution à la connaissance plus parfaite des annexes foetales chez les reptiles; Reception du sac vitellin et de l'allantoide dans la cavité abdominale. *Arch. Ital. de Biol.*, xxi, 1894a. (Abstract from paper in *Monitore Zool. Ital.*, iv, No. 7, 1893.)

HAACKE, 1885.—Über ein neue Art uteriner Brutflege bei Reptilien. *Zool. Anz.*, viii.

HARRISON, 1926.—*Roy. Zool. Soc. N.S.W.*, iv, part 5.

HARRISON AND WEEKES, 1925.—On the Occurrence of Placentation in the Scincid lizard *Lygosoma entrecasteauxi*. PROC. LINN. SOC. N.S.W., l.

HEAPE, 1900.—The Sexual Season, *Quart. Journ. Micr. Sci.*, xliv.

HETT, 1924.—Das Corpus Luteum der Zauneidechse (*Lacerta agilis*). *Zeitschr. Mikr. Anat. Forsch.* 1 Band, 1 Heft.

HILL, 1897.—The Placentation of *Perameles*. *Quart. Journ. Micr. Sci.*, xl.

HUBRECHT, 1889.—The placentation of *Erinaceus europaeus*. *Quart. Journ. Micr. Sci.*, xxx.

JENKINSON, 1913.—Vertebrate Embryology.

LILLE, 1908.—The Development of the Chick.

MARSHALL, 1910.—Physiology of Reproduction.

MINOT, 1891.—A Theory on the Structure of the Placenta. *Anat. Anz.*, vi.

WEEKES, 1927.—A Note on Reproductive Phenomena in some lizards. PROC. LINN. SOC. N.S.W., lii. 2.

EXPLANATION OF PLATES XXXVIII-XL.

Plate xxxviii.

Fig. 1. Photomicrograph of section of omphaloplacental region of embryo collected during the second week of the gestation period.

Fig. 2. Photomicrograph of section of yolk-sac of a young embryo showing the down-growth of mesoderm into the yolk-sac.

Plate xxxix.

Fig. 3. Photomicrograph of section of yolk-sac of six weeks old embryo showing the dense coagulum with corpuscles and scale-like appearance.

Fig. 4. Photomicrograph of section of mature allantoplacental region showing apposition of maternal and foetal tissues.

Fig. 5. Photomicrograph of section of folded allantoplacental region present in one of the embryos examined.

Plate xl.

Fig. 6. Photomicrograph of section of yolk-sac of eleven weeks old embryo showing the enlarged endoderm cells, growth of allantoic tissue and shell membrane.

Fig. 7. Photomicrograph of section of allantoplacental region showing the junction of inner allantoic membrane with the chorio-allantoic membrane.

LEGENDS TO PLATES XXXVIII-XL.

A.C., allantoic cavity; AMN., amnion; B.V., blood vessels; C., coagulum; C.E., chorionic ectoderm; E. CYT., endodermal cytoplasm; E.C.E.C., enlarged chorionic ectoderm cell; E.E.C., extra-embryonic coelome; E.N. E.C., enlarged endoderm cell; F.C., foetal capillary; F.F.T., folded foetal tissue; F.GR., finger-like growth; GR. T., growth of tissue; I.A.M., inner allantoic membrane; M.C., maternal capillary; P.S.C., peculiar shaped cells; SP. M., splanchnic mesoderm; SC. M., scale-like material; SO. M., somatic mesoderm; S.M., shell membrane; U.E., uterine epithelium; UT., uterus; Y.S., yolk-sac; Y.S.E., yolk-sac endoderm.